

Pollen wasps and flowers in southern Africa

Sarah K. Gess and Friedrich W. Gess







SANBI Biodiversity Series 18

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by

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Department of Entomology, Albany Museum
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Pretoria

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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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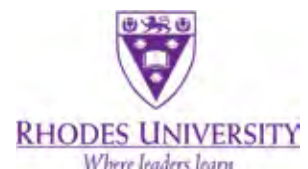


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Introduction

Why a book on pollen wasps as distinct from wasps in general and why in particular pollen wasps of southern Africa?

The pollen wasps are behaviourally distinct from all other aculeate (stinging) wasps. Indeed in behaviour they are bee-like. Like bees, they evolved from predatory wasps that, like most modern aculeate wasps, hunted insects or spiders for feeding their larvae. The pollen wasps, like the bees, are not hunters. They collect pollen and nectar from flowers for provisioning their nest cells. The change from hunting invertebrates to collecting pollen and nectar, evolved in parallel—the bees and the spheciform wasps being grouped as Apoidea and the pollen wasps and the co-evolved wasp families, including the ants, as Vespoidea.

Western southern Africa is particularly rich in pollen wasps where they are of importance as flower visitors and pollinators. Indeed it is the area in the world with the greatest species diversity of these wasps, the greatest number of which are associated with mesembs (Aizoaceae: Mesembryanthema) (45%) and/or composites (Asteraceae) (49%), both of which are similarly remarkably species diverse. In addition, and of particular interest, are the close associations of some other species of pollen wasps with other plants of which they are in many instances the sole or most dependable pollinators.

In 1996 a synthesis of the knowledge of the pollen wasps of the world was published as *The pollen wasps: ecology and natural history of the Masarinae*. This book by Sarah Gess gathered together all that was then known on biogeography, life history, nest-building behaviour, flower associations and associated organisms, and examined the role of these insects

as pollinators. It was the first synthesis of the nesting and flower visitation of pollen wasps since the publication of Owain Richards's 1962 monograph on the masarine wasps in which a brief six-page synthesis was presented. The bulk of information on southern African pollen wasps was derived from the studies of aculeate wasps and bees in southern Africa undertaken by Fred and Sarah Gess over the previous 25 years. At that time their studies had not yet extended into the northern Richtersveld and Namibia, the areas in which they have concentrated their field studies over the past 10 years. These studies have added considerably to the knowledge of pollen wasp diversity, distributions, nesting and flower associations, making a new synthesis for southern Africa of particular value. The cut-off date for the present synthesis is December 2008.

There is a misconception amongst many botanists concerning the abundance of pollen wasps. It is often suggested to us that they are rare. In fact, where they are present, they may be very numerous. Indeed, those species that visit water and excavate nesting burrows in the ground can be observed in their thousands at water and also in their nesting areas. They and nonwater-visiting species may furthermore be observed in large numbers visiting the flowers that they favour. There are several reasons for the misconception—they are often mistaken for bees, they are silent fliers, unlike many bees, wasps and beetles, they enter their flowers without any preliminary manoeuvring, unlike most flower visitors, and they are very alert and will leave a flower on the approach of an observer whereas most bees, beetles and many flies are far less readily alarmed.

World distribution

In 1996 Sarah Gess made certain generalisations from a consideration of the world distribution of the Masarinae, as deduced from the then published records. More recent investigations in no way change that understanding of world distributions. That is, masarines have not been found to occur further north than

50°N or further south than 50°S. Within these limits they have, furthermore, not been recorded from eastern North America or from eastern and southern Asia. Records are concentrated in Mediterranean and temperate to hot semi-arid to arid areas outside the tropics (Figures 1 and 2). These areas exhibit a north-

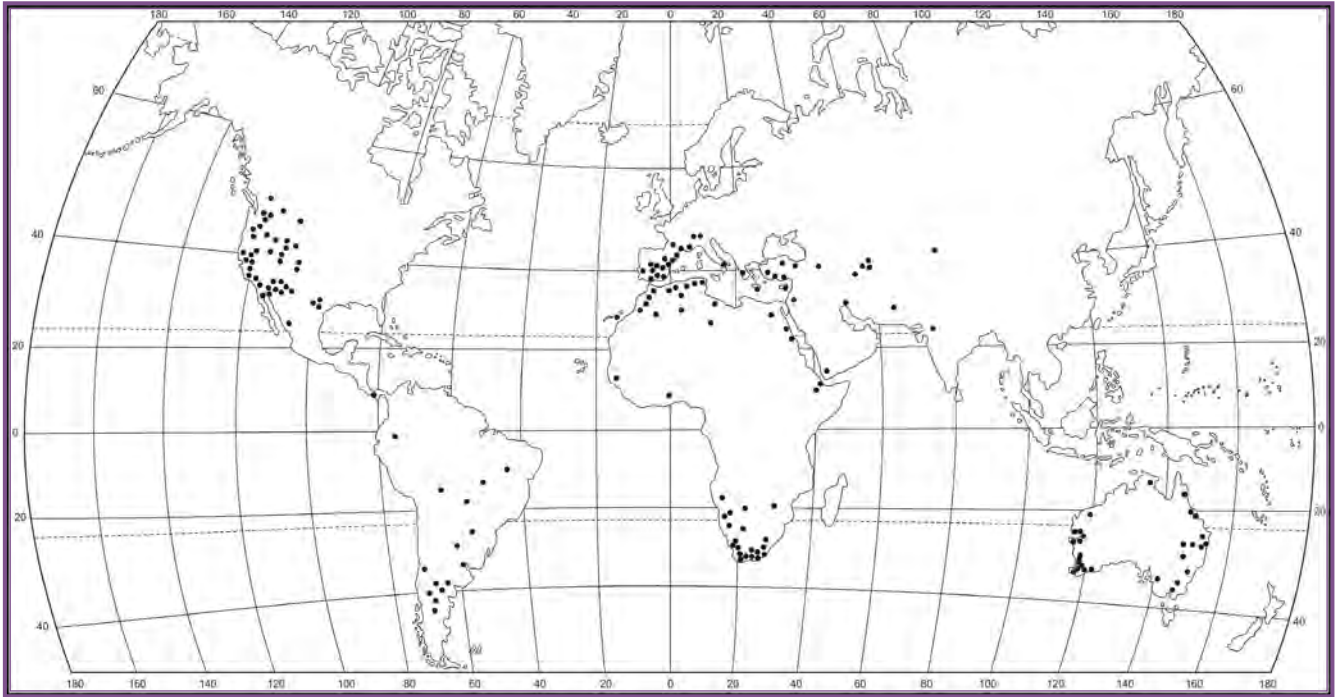


FIGURE 1. The world distribution of Masarinae based on published records (updated from Gess, S.K. 1996).

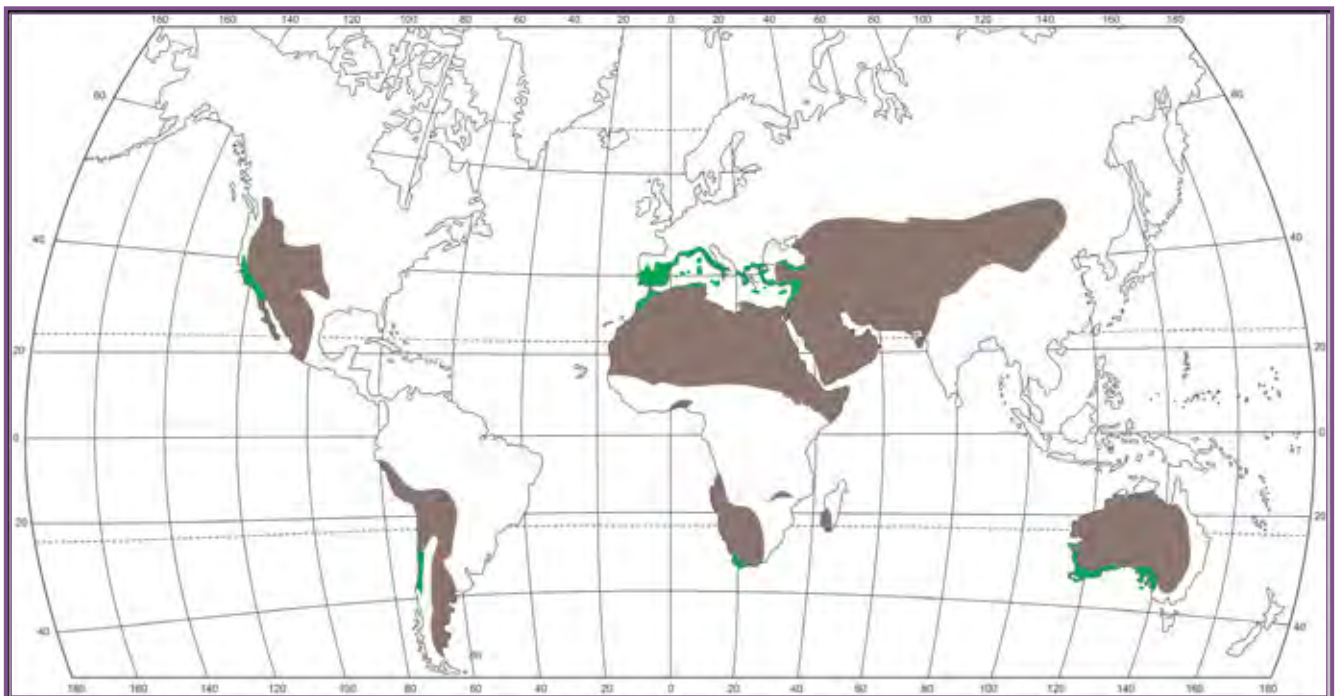


FIGURE 2. The distributions of the Mediterranean (green) and the temperate to hot, semi-arid to arid (brown) areas of the world, as defined in di Castri, Goodall, and Specht (1981), Evanari *et al.* (1985, 1986), and West (1983) (from Gess, 1996).

to-south, south-to-north and/or west-to-east macrogradient in which winter rains diminish and summer rains increase. Between such areas there is a broad similarity in the vegetation types, which replace each other along the macrogradient from Mediterranean climates to extreme deserts—from a dense maquis (termed fynbos in southern Africa) on the mesic side of the gradient the vegetation becomes progressively more open, low and sparse.

The representation of genera and species by Geographical Region is given in Table 1. Of the total number of species, 78% occur in the Afrotropical and Palaearctic regions combined, 47% in the Afrotropical Region and 31% in the Palaearctic. The remaining 22% of species are 10% Australian, 7% Neotropical and 5% Nearctic. Of the 151 species recorded from the Afrotropical region, 144 are restricted to southern Africa.

Southern African distribution

In 1996, Sarah Gess stated that the pollen wasps in southern Africa are largely confined to the Fynbos, the Succulent Karoo and Nama-Karoo Biomes and that the nodes of greatest diversity are located in the western and southern Karoo and in the southwest

at the interface between the Karoo and the Fynbos. Our intensive and extensive sampling in Namibia has greatly increased the knowledge of the species representation and distribution of pollen wasps in that country, demonstrating a greater diversity of species than was anticipated but not appreciably changing the overall picture, apart from demonstrating widespread occurrence in areas of extreme aridity and areas with unpredictable, annually infrequent rainfall, that is in the Namib Desert in the west and the Kalahari in the southeast respectively (Figure 3).

Recent delimitations of the biomes represented in southern Africa (Figures 4, 5–20) and comprehensive studies of their ecological patterns and processes have been presented in Cowling *et al.* (1997) and developed further for the Karoo in Dean & Milton (1999). The vegetation of each of the biomes is by no means uniform throughout a biome and can be divided into vegetation types related to, among other factors, altitude, geology and rainfall patterns. However, some generalisations can be made.

The Nama-Karoo is the largest of the three biomes included in the Karoo-Namib Region. Its annual rainfall varies, but as a

TABLE 1. Currently accepted classification of the Masarinae and the representation of taxa in geographical regions

Tribes	Subtribes	Genera	Number of species by Zoogeographic Region
Gayellini		<i>Gayella</i> Spinola	6 Neotropical
		<i>Paramasaris</i> Cameron	4 Neotropical
Masarini	Priscomasarina	<i>Priscomasaris</i> Gess	1 Afrotropical
	Paragiina	<i>Metaparagia</i> Meade-Waldo	9 Australian
		<i>Paragia</i> Shuckard	25 Australian
	Masarina	<i>Celonites</i> Latreille	34 Palaearctic 26 Afrotropical
		<i>Ceramiopsis</i> Zavattari	2 Neotropical
		<i>Ceramius</i> Latreille	15 Palaearctic 19 Afrotropical
		<i>Jugurtia</i> de Saussure	10 Palaearctic 25 Afrotropical
		<i>Masarina</i> Richards	13 Afrotropical
		<i>Masaris</i> Fabricius	5 Palaearctic
		<i>Pseudomasaris</i> Ashmead	5 Nearctic
		<i>Quartinia</i> Ed. André	37 Palaearctic 67+ Afrotropical
		<i>Trimeria</i> de Saussure	9 Neotropical
		All genera combined	151 Afrotropical 34 Australian 15 Nearctic 21 Neotropical 101 Palaearctic 322 total



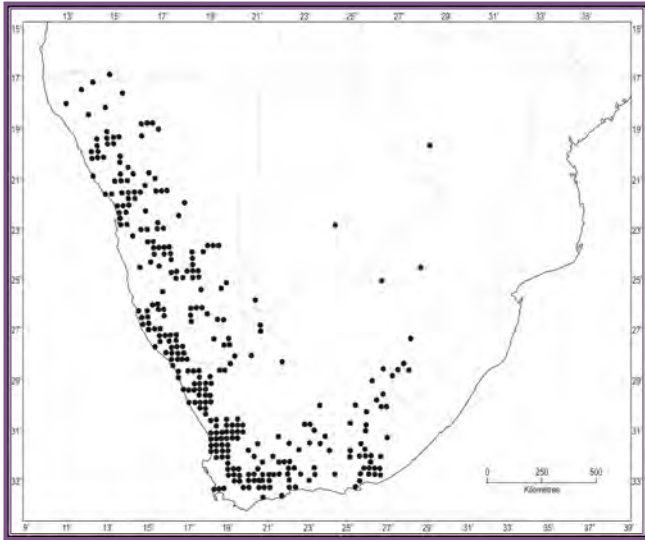


FIGURE 3. Known distribution of Masarinae in southern Africa based on published and unpublished collection records.

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 nonfriable, 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 (*sensu lato*) and Scrophulariaceae, the composition of the vegetation varying 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.

The Succulent Karoo is characterised by predominantly winter rainfall, by a remarkably high diversity of leaf succulents, particularly notable being the Aizoaceae: Mesembryanthema, the most species-rich 'taxon' in the southern African flora with its greatest species diversity in this biome, by being unusually rich in geophytic and leaf-succulent, petaloid monocots, and by having a scarcity of tall shrubs, trees and grasses. It is noted for the diversity of succulent species, unparalleled elsewhere in the world.

The Namib Desert stretches for 2 000 km in a north-south direction. It is adjacent to the Nama-Karoo and Succulent Karoo Biomes and can 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 those with a relatively dense 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 that germinate only when rain falls at a specific time of year) and ephemerals (plants that germinate whenever there is

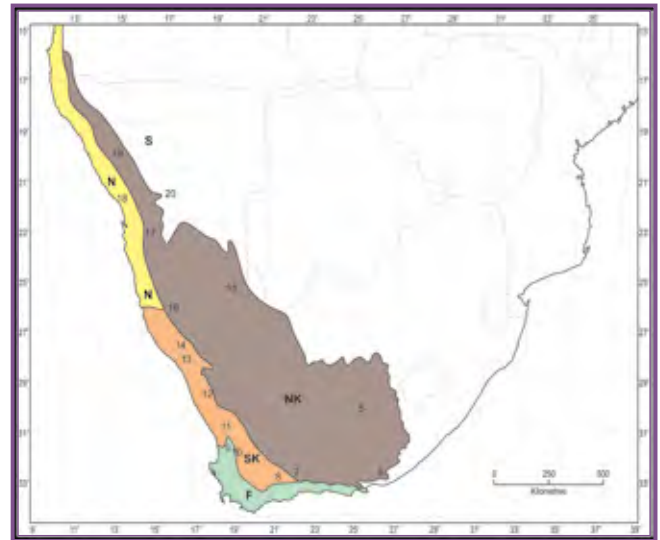


FIGURE 4. Southern Africa. The distribution of Fynbos (F; green), Succulent Karoo (SK; orange), Nama-Karoo (NK; brown), Namib Desert (N; yellow) and Savanna (S; after Rutherford (1997). Digits 5–20 denote areas illustrated in Figures 5–20.

sufficient moisture, irrespective of season) are notable. In the Namib, the annual and ephemeral flora differs greatly between regions. Some habitats such as the zones of minimum vegetation support these species only. In the Succulent Karoo portion of the Namib, geophytes are also of note.

The Fynbos Biome is typified in the main by a Mediterranean climate, that is by warm, wet winters with westerly winds and hot, dry summers, but in the southeast the rainfall changes to nonseasonal. The biome includes not only fynbos but also two other major vegetation types, renosterveld and a mosaic of fynbos and strandveld. Fynbos has been characterised as an evergreen, fire-prone shrubland, confined largely to sandy, infertile soils, and characterised structurally by the universal presence of restioids, a



FIGURE 5. Nama-Karoo, Colesberg.

high cover of ericoid shrubs and the common occurrence of an overstory of proteoid 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 also represented as an 'island' in Succulent Karoo in southern Namaqualand.

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



FIGURE 6. Eastern extension of Nama-Karoo, northwest of Grahamstown.



FIGURE 7. Interface between the Succulent Karoo and the Nama-Karoo, Prince Albert.



FIGURE 8. Western Little Karoo, near Ladismith.



FIGURE 9. Dry Fynbos to the west of the Olifants River Valley, Clanwilliam Dam in the distance.

Savanna is a tropical vegetation type, 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 and falls in summertime, between October and April. Savanna grades into the arid shrublands of the Nama-Karoo in the Eastern Cape, 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.

The Kalahari 'desert' 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 with the single largest body of wind-blown sand in the world. Over much of its area it is furthermore characterised by linear dunes, the crests of most stabilised with a permanent vegetation cover.



FIGURE 10. Karroid area in the Olifants River Valley, east of Clanwilliam at the foot of the Cederberg.



FIGURE 11. Succulent Karoo, Knersvlakte, Namaqualand.

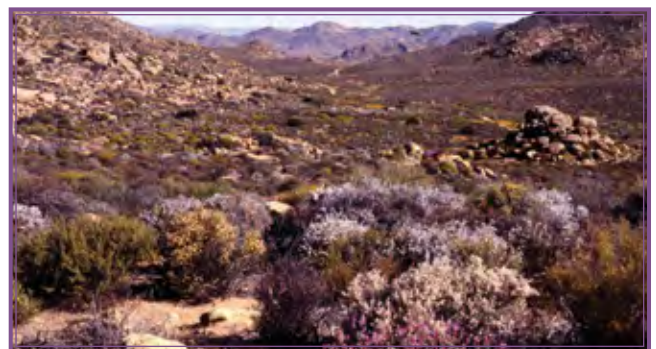


FIGURE 12. Namaqualand Broken Veld, Goegap, Springbok, Namaqualand.



FIGURE 13. Succulent Karoo, Koeroegabvlakte, Richtersveld National Park, Namaqualand.



FIGURE 17. Drainage channel, east of Walvis Bay, central Namib Desert.



FIGURE 14. Southern Namib Desert, south of Rosh Pinah.

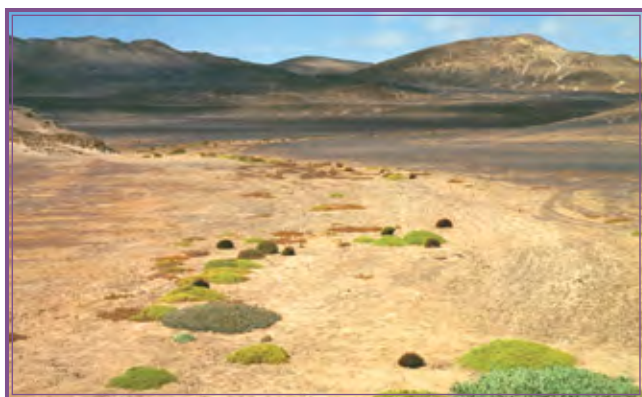


FIGURE 18. Drainage channel, north of Cape Cross, central Namib Desert.



FIGURE 15. Kalahari fringe, near Kōes.

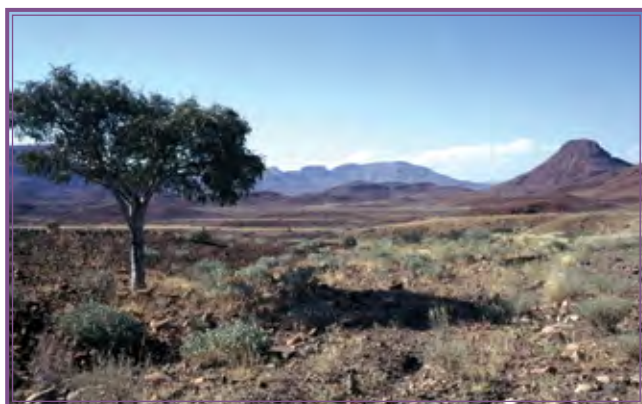


FIGURE 19. Nama-Karoo, in the vicinity of Khorixas.



FIGURE 16. Interface between Nama-Karoo, Succulent Karoo and Desert, near Aus.



FIGURE 20. Dry Savanna, west of Gross Barmen.

Morphology of pollen wasp mouthparts

Evolution of elongate suctorial mouthparts has occurred separately in several lineages of Hymenoptera, at least twice in the Masarinae, in association with the uptake of floral nectar. The manner in which the elongation has been achieved differs between taxa. In the pollen wasps, the proboscis is formed only by the glossa. Again whether or not elongation has taken place or the manner in which elongation has been achieved, differs between taxa. There has been no elongation of any part of the glossa in *Priscomasarina* (Figure 21), elongation of the distal portion has taken place in *Paragiina* and of the proximal portion in the *Masarina* (Figure 22). The glossa is retractable and in some species it is looped back into the glossal sac, the prementum, when in repose. The elongation of the proboscis is accompanied by the presence of lamellae on the anterior glossa leading to the formation of a median canal between the lamellae, considered to be homologous with the rows of 'hair structures' on the glossa of other Vespidae. The lengthening of the anterior lingual plate seems to be necessary for the development of mechanisms enabling the extension of the glossa out of the glossal sac. Uptake of nectar or water by pollen wasps takes place through slit-like openings in the canal of the glossal lobes, no pre-suction nectar loading being necessary, as required in the case of bees. In the long tongue of bees, the glossa is enclosed within the tube, which must first be loaded with nectar by means of glossal movements and capillary action before it is drawn through the tube by suction.

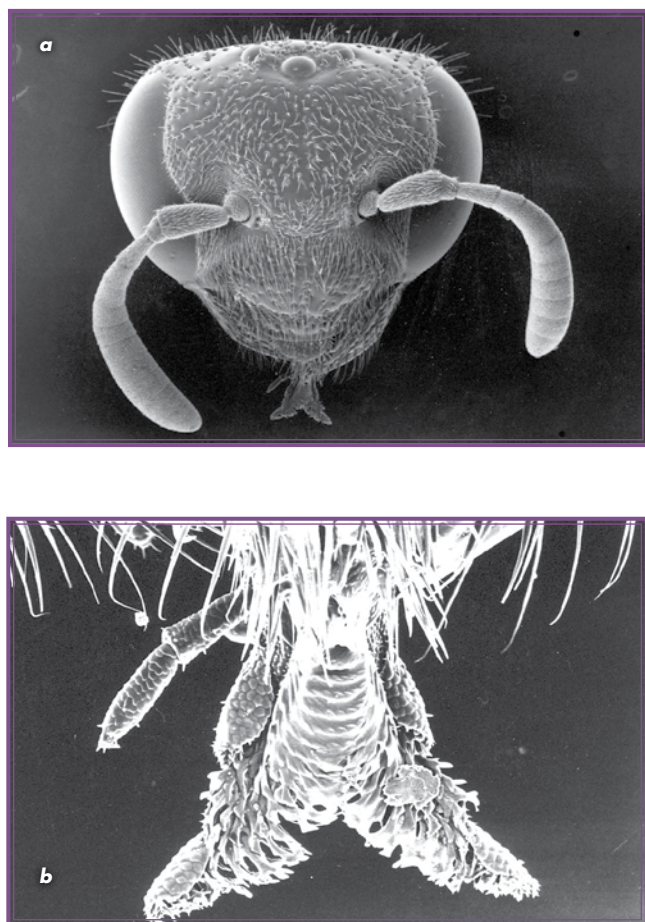


FIGURE 21. *Priscomasarina namibiensis* (Priscomasarina): a. head of female (actual width of head $\pm$ 2 mm); b. glossa of female (actual length of tongue $\pm$ 0.34 mm).

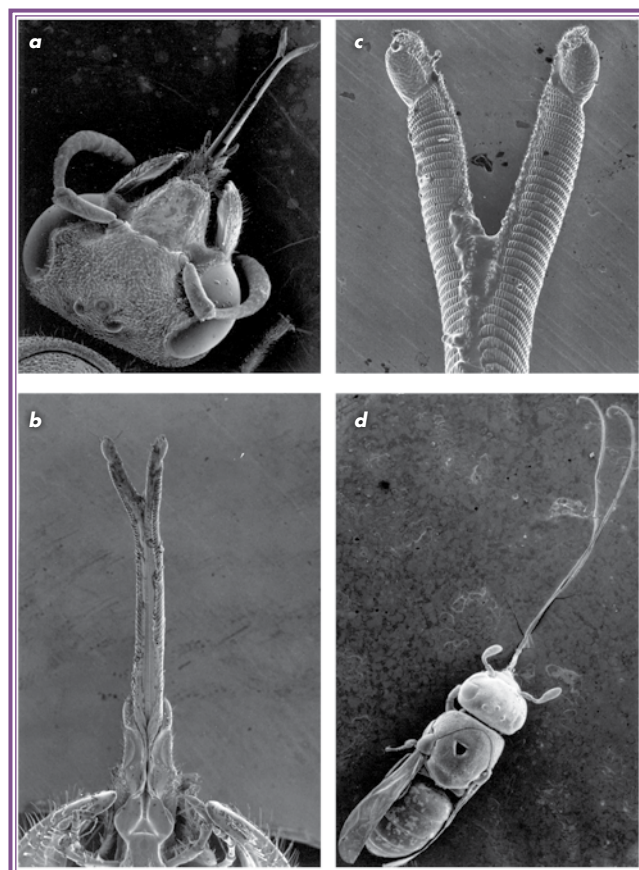


FIGURE 22. *Ceramius clypeatus* (Masarina): a. an example of a relatively short-tongued masarine wasp, dorsal view with tongue extended (actual length of tongue $\pm$ 5.68 mm); b. glossa, ventral view; c. dorsal view of portion of tongue to show lamellae. d. *Quartinia laeta* (Masarina), an example of a relatively long-tongued masarine wasp, dorsal view with tongue extended (actual length of tongue $\pm$ 4.88 mm).

Taxonomy

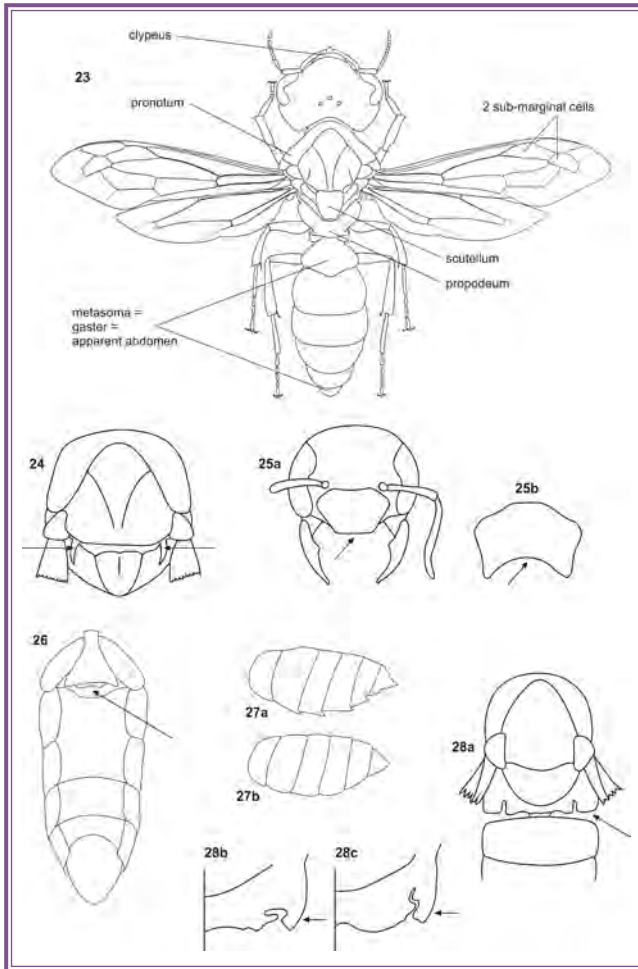
The pollen wasps are currently considered to constitute a sub-family, the Masarinae, of the family Vespidae, which in southern Africa is also represented by the subfamilies Eumeninae, which are mostly hunters of moth caterpillars although some species hunt beetle larvae, and Polistinae, social wasps that feed their larvae with macerated prey. Eumeninae are commonly known as potter wasps but this is misleading as pot-making is characteristic of only some of the genera. The Polistinae build comb nests from plant fibres that they macerate and transform into 'paper', hence they are commonly known as paper wasps.

The family Vespidae can be distinguished from other wasp families by the characteristic shape of the pronotum (Figure 23) and the Masarinae (except the extraterritorial tribe Gayellini) from the other subfamilies of the Vespidae by the possession of only two submarginal cells as compared with three in the Eumeninae and Polistinae.

All Eumeninae and Polistinae show longitudinal folding of their wings when at rest and in death but in the Masarini only *Celonites* and *Quartinia* show longitudinal folding of the wings. Thus *Priscomasarina*, *Ceramius*, *Jugurtia* and *Masarina* can be readily distinguished from the other Vespidae encountered in southern Africa.

The marked retractability of the gastral segments characteristic of the Eumeninae and Polistinae is absent in the Masarinae.

The currently accepted classification of the Masarinae is shown in Table 1 together with representation of taxa in geographical regions.



FIGURES 23–28. 23. Diagrammatic drawing of *Ceramius lichtensteinii* as a guide to morphological structures referred to in the text and key. 24–28. Diagrams illustrating characters given in key.

Key to subtribes and genera of Masarinae occurring in southern Africa:

- 1 Tongue very short; scutellum triangular, roundly pointed posteriorly, with its anterolateral angles conspicuously produced backward into outwardly convex and apically pointed processes (Figure 24); integument of the metasoma very shiny, reddish, with a pattern of large pale spots. Length $\pm$ 7 mm. One species only (*P. namibiensis* Gess); restricted to Namibia
..... Priscomasarina *Priscomasaris* Gess
- Without the above combination of characters. Tongue long to very long; scutellum without processes 2 (Masarina)
- 2 Clypeus ventrally truncate (i.e. cut off, straight) (Figure 25a) or gently convex; larger species (10–20 mm long) *Ceramius* Latreille
- Clypeus ventrally emarginate (i.e. concave) (Figure 25b); smaller species (5–12 mm; most shorter than 10 mm) 3
- 3 Forewings at rest (and in death) not longitudinally folded 4
- Forewings at rest (and in death) longitudinally folded 5
- 4 Sternum II (that is the underside of segment II of the metasoma or apparent abdomen) with a transverse furrow (Figure 26); sexual dimorphism marked *Jugurtia* de Saussure

Sternum II (that is the underside of segment II of the metasoma or apparent abdomen) lacking a transverse furrow; sexual dimorphism slight *Masarina* Richards

- 5 Terga (that is the upper side of segments of the metasoma or apparent abdomen) laterally acute (Figure 27a); sterna (that is the underside of the metasoma or apparent abdomen) depressed; propodeum with posteriorly directed lamellate processes (Figure 28) *Celonites* Latreille
- Terga (that is the upper side of segments of metasoma or apparent abdomen) laterally rounded (Figure 27b); sterna (that is the underside of the metasoma or apparent abdomen) rounded; propodeum without lamellate processes. Length 2–7 mm; great majority within lower half of the range
..... *Quartinia* Ed. André

Life history

Pollen wasps exhibit the usual holometabolous development of egg–larva–pupa–adult. The egg, larval and pupal stages are passed enclosed within a cell, part of a multicellular nest. The nests, depending on the identity of the female builder, are excavated in the ground or in vertical earthen banks or are constructed aerially on stones or plant stems or in a pre-existing cavity. The bonding agent used, again depending on the identity of the builder, is water, nectar or self-generated silk. No pollen wasps have been found to be nest parasites.

The formation of nesting aggregations is usual for ground-nesting species. This could result from the congregation of unrelated nesting individuals or from a tendency for individuals to nest in close proximity to their natal nests. The latter is demonstrated by nest aggregations of the single species of *Priscomasaris*, most species of *Ceramius* and a species of *Masarina* in which re-used multicellular nests with multiple emergences, each occupied by a single female, are found associated with new nests.

Most nesting studies indicate that nest construction, egg laying and provisioning are performed by a single female per nest. However, nest sharing has been suggested for some species. As nests are re-used, it is conceivable that with a breakdown in territorial aggression, nest sharing could occur. Indeed some flexibility in the behaviour of *Ceramius lichtensteinii* for which nest sharing was suggested by Hans Brauns (1910), has been noted by us; mud-pellets discarded during nest excavation were dropped outside the limits of the nesting aggregation at one locality whereas at other localities they were dropped amongst the nests.

Pollen wasp eggs are relatively large for wasps' eggs but relatively small compared with bees' eggs. The ratios of egg length to female length for random samples of wasps, pollen wasps and bees are 1:5.4; 1:3.3; and 1:1.5. Masarines oviposit into an empty cell before provisioning takes place, as do all the other vespids and some of the nyssonines. They therefore differ from most aculeate wasps and most bees, which oviposit onto the provision in a partially or fully provisioned cell. In common with most aculeate wasps and bees, a single egg is laid in each cell. It is positioned at the blind end of the cell either lying free as in the ground-nesting *Ceramius*, *Jugurtia* and *Masarina strucki*, and *Paragia* in Australia, or glued to the wall at the blind end in *Priscomasaris* nesting in the ground, in *Masarina familiaris* nesting in vertical banks, in the aerial nesting *Gayella* in Central America and in *Pseudomasaris* in North America.

Cell provisioning follows egg laying. The provision, unlike that of all nonmasarine wasps but like that of most bees, is constituted of pollen and nectar. Pollen wasps transport the provision internally in the crop like the colletid bees of the subfamilies Euryglossinae and Hylaeinae but unlike most bees, which carry pollen loads for provisioning externally. Mass provisioning is the general rule, although progressive provisioning has been alleged for *Trimeria howardi* Bertoni in South America and by Hans Brauns (1910) for *Ceramius lichtensteinii* in southern Africa. However, we have established that *C. lichtensteinii* practises mass provisioning, and, under optimal conditions of favourable weather and an abundance of forage flowers, provisioning and sealing of the cell is completed by the female before the egg hatches. Under less favourable conditions, the rate of provisioning is slowed down, leading to the finding of unsealed cells containing larvae and varying amounts of provision, and under really unfavourable conditions the situation is as reported by Brauns's results.

The egg phase, in common with all but the social wasps, lasts only a few days. Shortly before hatching the segmentation of the larva is visible through the pellicle.

The number of larval instars has not been recorded, but five is the norm for aculeate wasps and bees.

Feeding is completed during the final larval stage when all provision has been consumed. The larva then commences spinning a cocoon closely attached to the walls of the cell so that it is inseparable from them except, in some such as *Ceramius* at least, at the truncate outer end. Characteristic of wasps, defecation occurs only once during larval development, after spinning of the cocoon. The larva then becomes semiflaccid and markedly curved and enters a resting prepupal phase.

As in most solitary wasps and bees, it is the prepupa that overwinters. It enters a state of dormancy, the diapause. Pupation and emergence as an adult may take place in the following spring or summer, but it is possible for diapause to last for some years.

As a general rule at temperate latitudes, pollen wasps appear to be univoltine. However, evidence has been published that suggests that bivoltinism may occur in lower-latitude areas with summer rainfall and the findings for *Priscomasaris namibiensis* support this. The flight periods for pollen wasps in the semi-arid areas of southern Africa vary according to the climatic conditions prevailing in a particular year. Certain generalisations may, however, be made. In the winter-rainfall area in the west, emergence is earlier than in the east where the wettest seasons are spring and autumn. Thus emergences in the southwest start in August and peak activity can be expected in September/October. Thereafter, as the dry summer season advances, flowering of forage plants ceases and temporary pools dry up, resulting in a rapid drop in activity. By December it is over, except in the vicinity of permanent water where the flowering periods of forage plants are somewhat extended. In the south-east, earliest emergences are in late September and the greatest activity can be expected from early November to mid-December, depending on timing of rain. When rain is late, there is a shift to December–January or January–February. Late summer or early autumn rain has even resulted in a second but insignificant flush of nesting by *Jugurtia confusa* from February to early April. In the north, in the southern Kalahari and the semi-arid to arid summer-

rainfall areas of Namibia where localised thunderstorms can be expected in late summer, localised emergences of masarines and flowering of their forage plants are experienced. Collecting records for the Namib north of Swakopmund suggest that in this area some pollen wasps may fly during the winter months.

Associated organisms

Organisms here categorised as 'associated organisms' are those arachnids and insects that are ectoparasites, endoparasites, 'parasites' in nests, scavengers in cells or nest usurpers.

Ectoparasites

Acarina, mites

Examination of all the southern African genera of masarines revealed an association of mites with *Ceramius* alone. The mites were all hypopi (= heteromorphic deutonymphs) of the family Winterschmittiidae (= Saproglyphidae) (see Figure 52 under *Ceramius*).

Winterschmittiid mites are cosmopolitan and are richly represented in temperate or tropical zones of both hemispheres. Some are free-living on dead, decaying organic material, but most are insect associates living in the galleries of bark beetles and in the nests of solitary bees and wasps. The association with bees and wasps may be parasitic or symbiotic, the mites either sucking blood from but not harming the wasp prepupae and pupae or feeding on organic debris in the cells.

Endoparasites

Conopidae, thick-headed flies

Conopids, commonly called thick-headed flies, are commonly found on flowers. Their larvae are endoparasites in adult bees and wasps.

'Parasites' in nests

Mutillidae, velvet ants

Mutillids, commonly called velvet ants (see Figure 53 under *Ceramius* and Figure 96 under *Quartinia*), are larval ectoparasitoids of terrestrial immatures of other insects. They have been reared from fully fed larvae or pupae of a wide variety of bees and wasps within cells and/or cocoons.

Chrysididae, cuckoo wasps

All species of chrysidids, commonly called cuckoo-wasps, are 'parasitic'. The nature of the host is practically a subfamilial character in Chrysididae. The chrysidine genera *Allocoelia* (Allocoeliini) (see Figure 54 under *Ceramius* and Figure 97 under *Quartinia*), *Chrysis* (Chrysidini), *Chrysirissa* (Chrysidini) and *Spintharina* (Chrysidini) are associated with masarines. *Allocoelia* of the monogeneric tribe Allocoeliini occurs in southern Africa, specifically in Namibia, Zimbabwe and South Africa. Evidence that suggests an association solely between *Allocoelia* and pollen wasps is the fact that of the nine described *Allocoelia* species, seven have been found in association with pollen wasp nests.

Meloidae, blister beetles

Adult meloid beetles, commonly known as blister beetles (see Figure 55), are flower feeders. The larvae of more than 76 species



feed on acridid eggs, and those of more than 34 species on the provision laid in by bees. The larvae of a few species are known to feed on the larval provision and larvae of aculeate wasps.

Nest usurpers

Megachilidae, leafcutter bees

In southern Africa, ground-nesting masarines are subject to usurpation of nests by megachilid bees.

Note on classifications used

In the present work, the classification of wasps and bees at superfamily level and of wasps at family level follows Goulet & Huber (1993), and the classification of bees below superfamily level follows Michener (2000).

The classification of the flowering plants followed in Gess (1996) was that of Cronquist (1988), but in our more recent publications and in this book we have followed 'The Angiosperm Phylogeny Group' (APG 1998). With the ongoing very active phylogenetic research on flowering plants, there is a continuous shift in understanding of the family boundaries. These changes can be followed on the Angiosperm Phylogeny Website at <http://www.mobot.org/MOBOT/research/APweb>.

The classifications of the flowering plants in Leistner (2000) and Germishuizen & Meyer (2003) mainly follow APG (1998), but not in all instances, and do not in all instances agree with each other. In the interest of clarity, the different interpretations of family limits for those plant 'families' visited by pollen wasps are given in Appendix 1.

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

Authors of southern African masarine species are given in the species lists, authors of masarine species and plant species are given in Appendices 2 and 3 and authors of other organisms are given in the text.

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Priscomasarina: Priscomasaris

Priscomasaris namibiensis, the only known species of *Priscomasarina*, is distinguished from other southern African pollen wasps by its very short tongue (glossa), antennae without an antennal club, the unique development of the scutellar (= axillary) processes, and the very shiny metasomal integument with a unique pattern of large pale spots situated posterolaterally on terga I–V and posteromedially on terga II–V.

Females are ± 8 mm long and the males ± 7 –8 mm. The range overlaps that of the smaller species of *Jugurtia* (± 7 –15 mm long), *Masarina* (5–9 mm long) and *Celonites* (5–9 mm long). There is, however, no overlap in distribution between *Priscomasaris* and *Masarina*.

The males are similar in general facies to the females (Figure 29). The antennae are somewhat longer and the mandibles are quadridentate, not tridentate.



FIGURE 29. A pair of *Priscomasaris namibiensis*, female on left (actual size ± 8 mm), male on right.

As in all genera other than *Celonites* and *Quartinia*, the wings do not fold longitudinally.

The ratio of tongue length to body length is 0.07, whereas for the species of *Masarina* it is 0.20–1.10.

A striking field character is that when collecting water, *P. namibiensis* alights on the water surface like some species of *Ceramius*, but unlike *Jugurtia* and *Masarina* which collect water from the edge of a water body. A second field character is the very shiny wings, held erect during water intake, that reflect the sunlight.

Distribution

Priscomasaris is endemic to southern Africa. It has a narrow distribution north of the Orange River where it has been found in what is seen as the northern tongue of the Nama-Karoo, as far north as Palm and south to Tses (Figure 30).

Flower visiting

Both females and males forage on flowers of species of *Gisekia* and *Limeum* (Molluginaceae) (Appendix 2) (see Figure 109 under 'Pollen wasps as flower visitors and potential pollinators'), for which their short tongues are adequate. We have also observed them drinking nectar from the extrafloral nectaries of *Euphorbia glanduligera* (Euphorbiaceae).

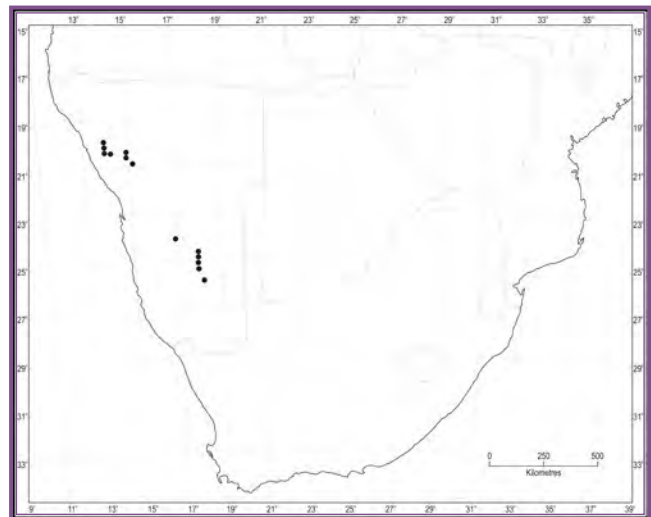


FIGURE 30. The known distribution of *Priscomasaris*.

Water visiting

Females visit pools of water in drainage channels and river beds to obtain water, apparently for use in nest construction. When they were common, very large numbers were present on and over the water. When filling their crops they always alight on the water surface, never at the water's edge. While on the surface, the wings are held erect.

Males were never observed at water.

Nesting

Nesting has been recorded for the single species, *P. namibiensis*.

Nesting areas and nest situations

Two nesting areas of *P. namibiensis* have been located, both in Dwarf Savanna Shrub, Nama-Karoo, to the east of the Mariental-Keetmanshoop road and railway track, one 5 km south of Mariental (Figure 31) and the other 7 km south of Gibeon railway siding. Both areas are associated with drainage lines that form part of the Fish River catchment. Rainwater pools, resulting from recent thundershowers, were present in association with the railway embankment through which the drainage channels have passage.



FIGURE 31. A nesting area of *Priscomasaris namibiensis* south of Mariental (24.40S, 17.57E) in Namibia.

The nests were aggregated above normal flood level within sparsely vegetated sites. In the Gibeon nesting area the two aggregations discovered were relatively small, of no more than 10 nests, 9–11 m from the water source. The soil was compacted sand with a sufficient clay element to make it malleable when mixed with water and with an inclusion of small pebbles. The gravelly surface was scattered with pebbles and small plants. Individual nests had been sighted next to a pebble or a small plant.

In the Mariental nesting area the very numerous nests were distributed over a site $\pm 100 \times 100$ m. The soil was compacted sand of an even consistency with a sufficient clay element to make it malleable when mixed with water. The surface, which was of firm sand, was stable and scattered with an occasional pebble and mat-forming plant. Most commonly the nests were grouped beneath or between the spreading branches of semiprostrate *Gisekia africana* (Molluginaceae) (Figure 32), a forage plant of *Priscomasaris*, and of a mat-forming species of *Indigofera* (Papilionaceae), the flowers of which it does not visit. Less commonly, the nests were exposed but were then positioned next to a pebble.



FIGURE 32. Nest entrance turret of *Priscomasaris namibiensis* among the branches of *Gisekia africana*.

Description of the nest

The nest of *P. namibiensis* consists of a multicellular subterranean burrow surmounted by a curved, tubular mud turret of the same diameter as the burrow opening and usually running parallel to the ground for most of its length (Figures 33–36). The main shaft is vertical and is of equal diameter for its entire length. At its base the main shaft curves outwards to form a short lateral shaft that terminates in a subhorizontal excavated cell in which is a constructed mud cell. A second cell terminates a similar lateral shaft which leaves the vertical shaft at the same depth but at an acute angle from the first such that the two cells lie close together. Further cells in similar pairs are positioned almost immediately below the first pair, each pair deeper than the preceding one, so that the cells form a 'stack' to one side of the main shaft. The largest number of cells recorded was 13.

Method of construction of the nest

When excavating a burrow, *P. namibiensis* extracts soil as moist mud pellets. As nest-constructing females make frequent visits to water, it is almost certain that it is regurgitated water that is used for moistening the soil.



FIGURE 33. *Priscomasaris namibiensis* with nest entrance turret: a and b. preparing to enter nest entrance turret; c. entering nest entrance turret, ventral surface uppermost; d. preparing to leave nest to discard the mud pellet held between mandibles; e. flying away from nest with mud pellet, which will be dropped in the pellet dropping area; f. adding mud to the rim of entrance turret. Actual length of wasp ± 8 mm.



FIGURE 34. Entrance turret of *Priscomasaris namibiensis* on right, discarded mud pellets on left, among the branches of a species of *Indigofera* (Papilionoideae) not used as a forage plant.

At an early stage in shaft excavation, the entrance turret is constructed from pellets extracted from the burrow. These are laid down around the rim of the entrance to the burrow in such a way that the inner diameter equals that of the main shaft, that is 3 mm. At the outset of turret construction, the thickness of the wall is ± 1 mm but after the turret has reached a height of a few millimetres it is reduced to 0.5 mm. After the turret reaches a height of ± 6 mm, pellets are usually added in such a way that the turret curves over, typically until the opening is vertical, after which they are added evenly around the circumference so that the resultant tube is horizontal, running parallel to the ground for a further 13–17 mm, separated from it by a gap of ± 2 mm. As the turret matches the colour of the soil, it is well camouflaged. Together with its concealed position beneath or between the spreading branches of a plant or up against a pebble or the base of a plant, this makes the nest difficult to spot.

When entering a nest, a female, alights on the upper surface of the entrance turret facing towards the opening and enters by curving over the lip so that, when progressing along the passageway, she is ventral surface uppermost (Figure 33a–c). When leaving the nest during shaft excavation, she emerges posterior end first, dorsal surface down, and climbs out onto the upper surface (Figure 33d, e) so that before flying away she faces towards the opening, in fact exactly replicating her entry in reverse. While adding mud to the turret, she remains curved around the rim (Figure 33f), progressing around it in a constant direction.

When discarding a pellet, a female, holding the pellet in her mandibles, flies in a roughly circular path, dropping the pellet at the furthest point from the nest, which may be 10–30 cm. Usually the variation in distance of an individual's flight path is not more than 7 cm so that the pellets accumulate in a small area (Figure 34).

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 describes a smooth curve and after ± 5 mm is expanded to form an excavated cell ± 1.5 mm long 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

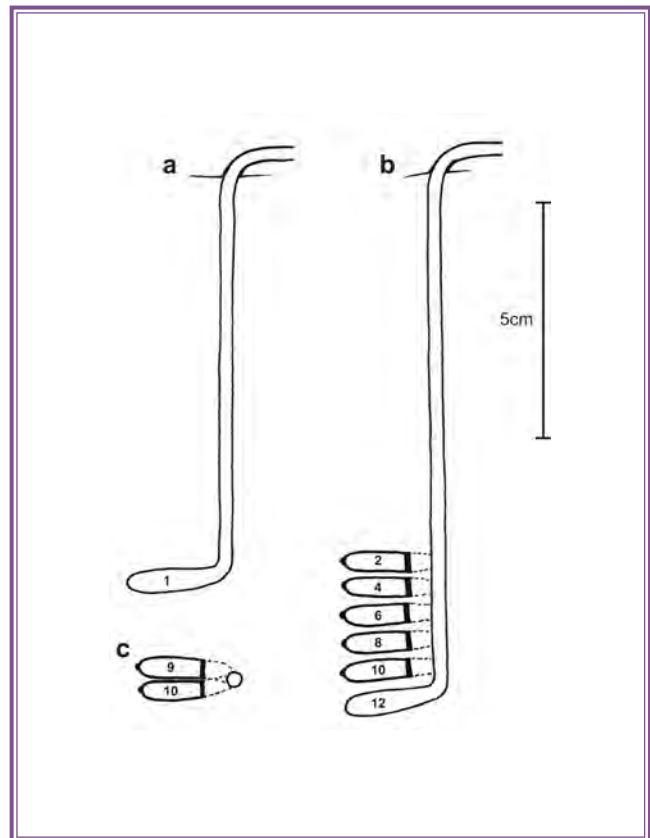


FIGURE 35. Plans of two nests of *Priscomasaris namibiensis*: a and b. vertical in single plane, a. nest with first cell only, b. nest with 12 cells; c. transverse in single plane.

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 smoothed. 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, not ovoid (Figure 36).

The source of soil for the construction of the cells was not determined. No quarry site within the nest was found. In nests with newly constructed open cells there did not appear to be an excavated or partially excavated cell that could have been the source. As there is no turning 'bulb', such a source is also eliminated. The builders were carefully observed and were not bringing in soil from outside the nest. On numerous occasions, when investigating and opening up nests, loose dry soil was found in the shaft from a depth of 50 mm downwards. There was no way that this soil could have fallen into the shaft. It is therefore possible that, when a cell is excavated, the soil extracted is not carried out as pellets but stored loose in the shaft and that the female coming and going from the nest can pass through the loose soil. This soil would then be available for cell construction.

The cell walls appear to be harder and more brittle than those of the turret. This suggests that either, as in drying of concrete, slower drying of the mud used in cell construction results in a 'stronger' cementing or that something other than water is added to the mud mixture. As *Celonites* and *Pseudomasaris* use nectar for bonding soil used in construction of cells, nectar was considered a possibility. One gram of cell wall was tested for sugar content. Total sugars extracted amounted to only 3 milligrams,

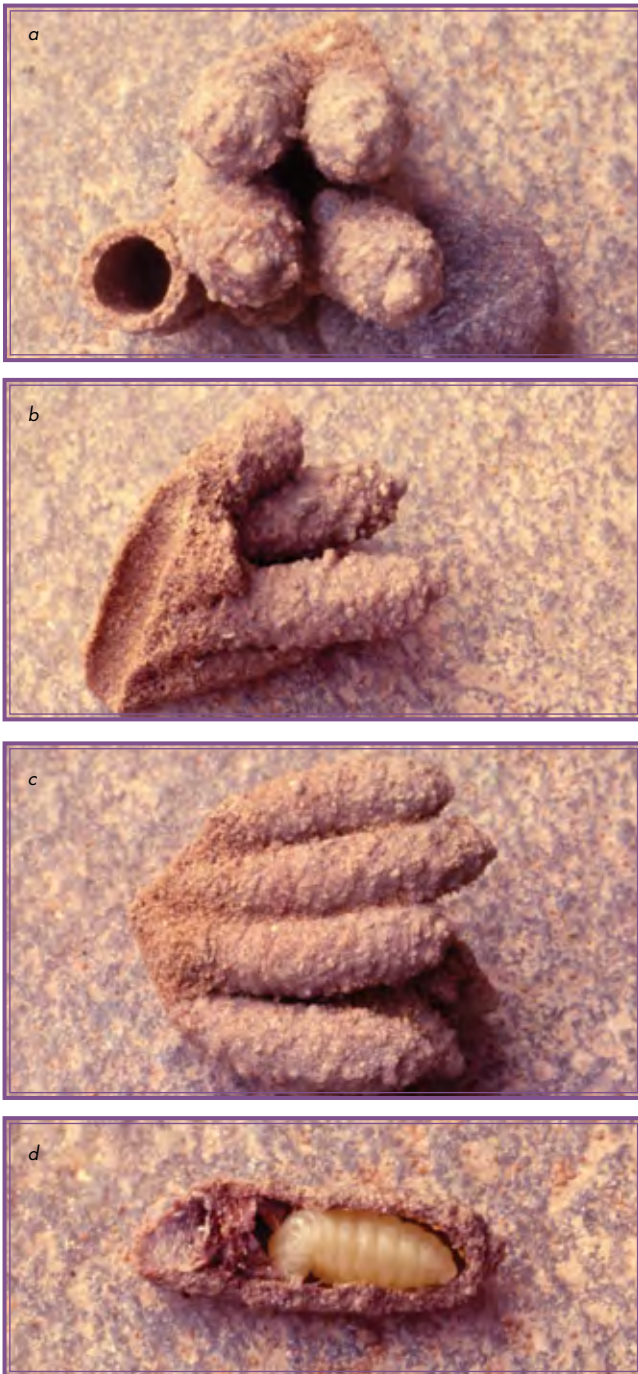


FIGURE 36. Nest burrow and constructed mud cells of *Priscomasaris namibiensis*: a. burrow cut in vertical plane; b. constructed mud cells, four viewed end on (note papillate inner end of mud cells) and one cut transversely to show thickness of cell wall and smoothed inner surface; c. group of constructed mud cells sealed off from cut main shaft, which is shown cut vertically; d. constructed mud cell cut longitudinally, showing full grown larva and silken parchment-like closure.

0.6 micrograms of which were found to be glucose and 0.8 micrograms fructose. This is considered too low a concentration of sugars to suggest deliberate use of nectar and therefore should be considered rather to be accidental addition from the crop which is used variously to carry nectar and water.

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 that 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 (Figure 36c).

A first cell having been completed and sealed off, a second lateral shaft leading to a second cell is excavated at the same depth and in the same plane as the first, but at an acute angle from it.

On completion and sealing off of this cell, a third lateral shaft with a 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 subhorizontal cells forms to one side of the vertical shaft.

Of the 22 nests investigated at Mariental on 10 March 2000, five (22.7%) had not yet reached the stage of lateral shaft excavation, four (18.2%) had reached lateral shaft excavation but not cell excavation, six (27.3%) had one cell each, and five (22.7%) had two cells. Twelve days later 12 nests were investigated: four (33.3%) had one cell each, one (8.3%) two cells, two (16.7%) three cells, two (16.7%) four cells, one (8.3%) 11 cells, and one (8.3%) had 13 cells.

Taking two as possibly the largest number of cells per nest on 10 March and 13 twelve days later, it is estimated that it is possible that a cell could be prepared, oviposited into and provisioned in a single day. This is of course a very rough estimate but would be comparable with the rate observed for *Celonites latitarsis* and *Masarina strucki*.

Re-use of nests

No instances of re-use of nests have been recorded.

Provision

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 (Figure 36e). One complete 'pollen loaf' was 8.17 mm long 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 2000 were examined microscopically. Four distinct pollens of 17.5, 20, 25 and 30 μm in diameter were present. These were compared with pollens from flowers visited by *Priscomasaris* and were found to match those of *Trianthema parvifolia* (Aizoaceae) (Figure 106b), *Limeum argute-carinatum* (Molluginaceae), *Gisekia africana* (Molluginaceae) and *Sesuvium sesuvioides* (Aizoaceae) (Figure 106a) respectively. The proportions of the different pollens 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, sleeping or sheltering in the nest by females at night or in inclement weather seems to be common among the pollen wasps and is practised by *P. namibiensis*.

Male behaviour

No males have been found in nests or at water. In the morning, before the appearance of females, males fly to and fro over nesting aggregations and visit flowers. After females have made their appearance, males have been observed mounting them, both on the ground in the vicinity of nests and on flowers. Actual copulation has not been observed.

Associated organisms

No instances of any of the categories of associated organisms have been recorded.

Currently recognised species

P. namibiensis Gess, 1998

Literature consulted

Ecology and natural history

GESS, S.K. 2001. Distribution and ethology of *Priscomasaris* Gess (Hymenoptera: Vespidae: Masarinae: Priscomasarina) in Namibia. *Journal of Hymenoptera Research* 10: 16–28.

GESS, S.K. & GESS, F.W. 2003. *A catalogue of flower visiting records for aculeate wasps and bees in the semi-arid to arid areas of southern Africa*. Albany Museum, Grahamstown. 529 pp.

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GESS, S.K. & GESS, F.W. 2004. The distributions of the genera of the pollen wasps (Hymenoptera: Vespidae: Masarinae) in the semi-arid to arid areas of southern Africa in relation to their requirements for successful nesting. *Transactions of the Royal Society of South Africa* 59: 23–27.

Publications useful for identification of species

GESS, F.W. 1998. *Priscomasaris namibiensis* Gess, a new genus and species of Masarinae (Hymenoptera: Vespidae) from Namibia, southern Africa, with a discussion of its position within the subfamily. *Journal of Hymenoptera Research* 7: 298–306.

Masarina: *Ceramius*

The genus *Ceramius* has been divided into eight species groups on the basis of morphological characters, supported by nest structure and forage plant associations. With the exception of Groups 1 and 7, which are endemic to the Palearctic, all these species groups are endemic to southern Africa.

Most species of *Ceramius* can be distinguished from other southern African Masarinae on size, being generally larger than species of the other genera. The exceptions are the smallest species of *Ceramius*, *C. bicolor* ($\pm 10\text{--}11$ mm long) and the smallest individuals of *C. socius* ($\pm 11\text{--}15$ mm long). All other species of *Ceramius*, even small individual males, are longer than 12 mm and range up to ± 20 mm (*C. rex*).

Males are distinct in appearance from females, having markedly longer, generally downward and backwardly curved antennae (Figure 37), some species having processes ventrally on the gaster and some species being of distinctly different coloration.



FIGURE 37. Pair of *Ceramius rex*, female on left (actual length ± 20 mm), male on right.

The antennal club is tapered towards the base as in all genera other than *Celonites* and *Quartinia*, in which the antennal club is rounded.

As in *Priscomasaris*, *Jugurtia* and *Masarina*, the wings do not fold longitudinally like those of *Celonites* and *Quartinia*.

Tongue length in *Ceramius* is $\pm 3\text{--}6$ mm, with the ratio of tongue length to body length $\pm 0.2\text{--}0.3$.

Distribution

Ceramius has been recorded from the Nama-Karoo, from the east across the southern Great Karoo and the Little Karoo, the southwestern Fynbos, northwards through the Olifants River Valley, and from Namaqualand northwards to the Kunene (Figure 38). 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,

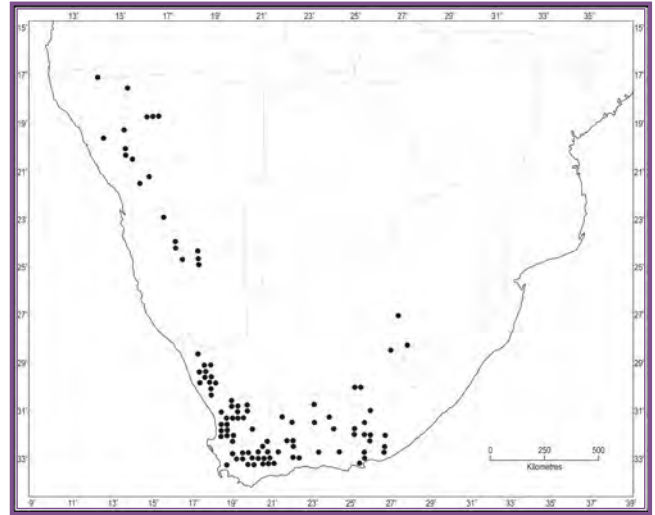


FIGURE 38. The known distribution of *Ceramius* in southern Africa.

on the fringes of the Etosha Pan and on the fringe of the arid savanna. *Ceramius* species to the south of the Orange River exhibit a variety of distributions from relatively widespread to extremely narrowly endemic.

Groups 5 and 8, all species of which forage on *Mesembryanthema* (Aizoaceae), are distributed throughout the greater part of the South African distribution range of the pollen wasps as a whole.

Group 4, both species of which forage on Aizoaceae, has a disjunct distribution, *C. beyeri* which forages on *Mesembryanthema* having a relatively wide southern distribution and *C. damarinus* which forages on non-*Mesembryanthema* having a relatively narrow distribution extending from southern Namibia to the Kunene.

Group 2A, two species of which forage on *Mesembryanthema*, has a western and southern distribution, *C. cerceriformis* being found throughout the distribution range of the group and *C. peringueyi* seeming to be the most restricted of the species foraging on *Mesembryanthema* having been recorded solely from north of the Olifants River Mountains to immediately south of Namaqualand.

Groups 3 and 6, all species of which forage on Asteraceae, are relatively limited in distribution. The individual species in Group 3 show very little overlap in their distributions, that of *C. nigripennis* being Namaqualand, that of *C. toriger* being inland of the Cederberg, that of *C. braunsi* being largely Olifants River Valley with one record from Willowmore in the southeast and that of *C. jacoti* being western Little Karoo. Those of Group 6 are discrete and very restricted, that of *C. caffer* being to the south of the Olifants River Mountains and to the east of the Cederberg, that of *C. metanotalis* to the north of these mountains but to the south of Namaqualand and that of *C. rex* being in the area of Namaqualand termed Klipkoppe.

The two species of Group 2B, *C. richardsi* and *C. clypeatus*, and the single species of Group 2C, *C. micheneri*, forage on Papilionaceae. *C. clypeatus* and *C. micheneri* seem to be restricted to *Aspalathus* and to a small area in and adjacent to the southern Olifants River Valley to the north of the Olifants River Mountains. *C. richardsi* has been recorded not only from the southern Olifants River Valley but also from south of the Olifants River Mountains.

From this survey of the distributions of the *Ceramius* species it can be concluded that although all southern African species of *Ceramius* are relatively narrowly endemic, most species associated with the Mesembryanthema group of the Aizoaceae are more widely distributed than those associated with Asteraceae and Papilionaceae. Furthermore, amongst the latter there are species that can be considered to be extremely narrowly endemic.

Flower visiting

Flower-visiting records are available for all 20 described southern African *Ceramius* species (Groups 2–6 and 8) (Appendix 2). Of these species, 45% have been recorded from the flowers of Asteraceae, 45% from the flowers of Aizoaceae, and 20% from the flowers of Papilionaceae. That the percentages for flower families visited is in excess of 100% is explained by records of occasional visits by some species to plants of families other than those preferred. Such visits appear to be for nectar only. For example, we have occasionally collected females of *C. braunsi*, a species showing a clear preference for Asteraceae, from flowers of *Aspalathus spinescens* (Papilionaceae). However, microscopic examination of pollen from the crop of such a female showed it to be entirely derived from flowers of Asteraceae.

Other plants recorded as being occasionally visited by *Ceramius* species in southern Africa are: *Wahlenbergia* (Campanulaceae) by *C. socius*; *Blepharis* (Acanthaceae) by *C. lichtensteinii* and *C. damarinus*; Zygophyllaceae by *C. brevitaris* and *C. damarinus*; and Lamiaceae, Molluginaceae and Scrophulariaceae by *C. damarinus*. Visits to *Wahlenbergia* flowers are not unusual for some other masarine genera, being the known preferred flowers of some southern African species of *Celonites* and *Quartinia* and a species of *Masarina*, and being occasionally visited by *Jugurtia*. Flowers of Acanthaceae are not otherwise visited by pollen wasps, though flowers of the closely related family Scrophulariaceae are preferred by some species of southern African *Celonites* and *Quartinia* and of the North American genus *Pseudomasaris*. Lamiaceae are visited by *Ceramius* and *Celonites* in the Palearctic and there are some secondary records of visits by *Pseudomasaris* to flowers of this family in North America.

Only two flower-visiting records (one each for a female and a male) have been obtained for *C. brevitaris* (Group 2A). These are both for *Zygophyllum prismatocarpum* (Zygophyllaceae), the first records of visits by *Ceramius* to Zygophyllaceae in southern Africa or the Palearctic.

Pollen from provision obtained from 15 *Ceramius* species was for each species derived from a single plant family. This indicates that the genus *Ceramius* is markedly oligophagous, provisioning with only Aizoaceae, Asteraceae or Cape Crotalariaeae according to species group.

A high percentage of species associated with Asteraceae and Aizoaceae is shared with southern African *Quartinia* and with respect to Asteraceae, with *Jugurtia*.

Recent studies of Palearctic *Ceramius* by Volker Mauss suggest that some of these species are polylectic.

(See figures under 'Pollen wasps as flower visitors and potential pollinators on page 59.')

Water visiting

All species found nesting were recorded as visiting water. In addition, *C. brevitaris* was found at water. All species studied fill the crop with water which, when regurgitated upon the clayey nesting substrate, makes the latter more easily worked and thus makes nest construction possible.

It seems that water-collecting behaviour is usually constant for species and species groups.

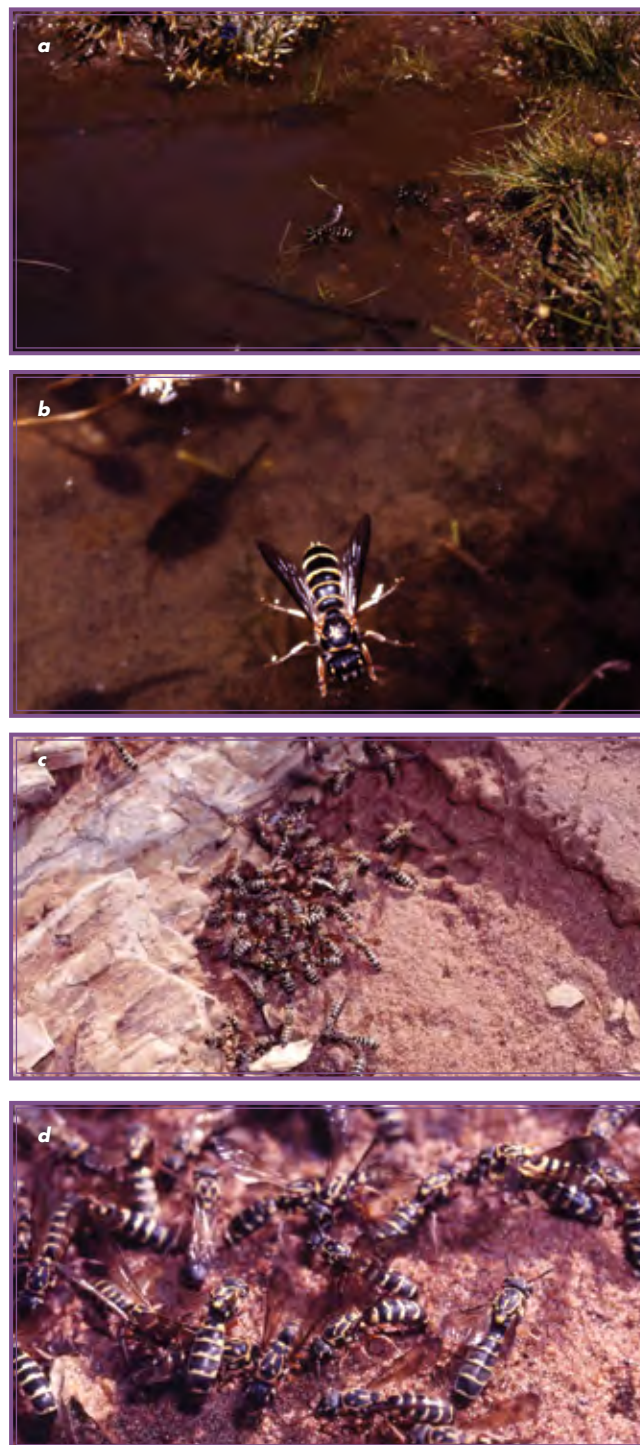


FIGURE 39. Water collection: a and b. female filling her crop with water while standing on the water surface a. *Ceramius rex* (actual size of female 20 mm), b. *C. nigripennis* (actual size of female 15 mm); c and d. aggregation of females filling their crops while standing on wet sand at water's edge, *C. socius* (actual length of females 13.5 mm).

All four species of Group 3, *C. nigripennis*, *C. jacoti*, *C. braunsi* and *C. toriger*, at least one species, *C. damarinus*, of Group 4 (water collection has not been observed for *C. beyeri*), the single species of Group 5, *C. lichtensteinii*, and two species of Group 6, *C. rex* and *C. metanotalis* (water collection has not been observed for the third species *C. caffer*), alight on the water surface to collect water (Figure 39a, b).

Four species of Group 2, *C. cerceriformis*, *C. clypeatus*, *C. richardsi* and *C. micheneri* (water collection has not been observed for the fifth species, *C. peringueyi*), alight at the edge of the water.

Group 8 seems to be exceptional in showing intra- and interspecific variation in water-collecting behaviour. *Ceramius linearis* alights on the water surface, *C. bicolor* and *C. socius* collect water from the damp soil at the water's edge and *C. capicola* seems to collect water either on the water surface or at the water's edge (Figures 39c, d).

Males are present at water-collecting sites.

Nesting

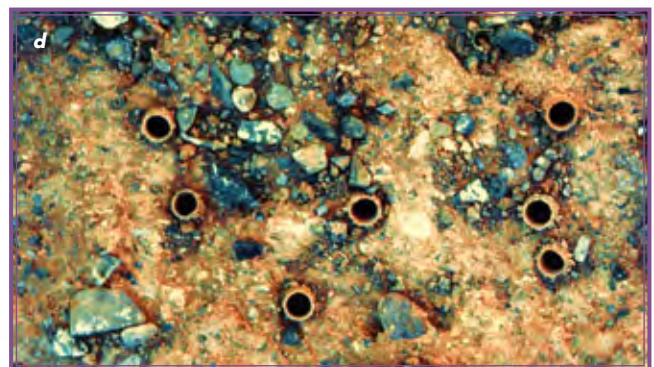
Nesting has been recorded for 16 of the 20 southern African species of *Ceramius*: *C. cerceriformis* (Group 2A); *C. clypeatus* (Group 2B); *C. micheneri* (Group 2C); *C. nigripennis*, *C. jacoti*, *C. braunsi* and *C. toriger* (all Group 3); *C. beyeri* (incomplete nest) and *C. damarinus* (both Group 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).

Nesting areas and nest situation

All nest in the bare ground (Figure 40) in relatively close proximity to their forage plants and a water source. *Ceramius* appears to show a preference for horizontally presented soil, though some species, *C. lichtensteinii*, *C. jacoti*, *C. braunsi*, *C. nigripennis* and *C. socius* at least, will nest in sloping ground. *Ceramius* species have never been found nesting in vertically presented soil.

The soil particle size varies from relatively coarse to very fine. In all instances the clay factor is sufficient to make soil malleable when mixed with water. Nests are aggregated in bare areas. The siting of nest aggregations varies from apparently random within a bare area to a definite positioning. Several different nesting sites have to be visited before a definite positioning can be assumed. The nests of *C. nigripennis* always seem to be in close proximity to the base of a bush, whereas those of *C. socius* may be fully exposed and massed in the centre of a large bare area or scattered in bare areas between the spreading branches of its forage plant. As with other ground-nesting aculeate wasps and bees in Namibia nesting in thornbush savanna, included in the selection of bare areas used for nesting by *C. damarinus*, was one at the foot of a termitarium of *Macrotermes mossambicus* (Hag.) (Figure 40c).

Right: FIGURE 40. Examples of *Ceramius* nesting areas: a. typical nesting area, a bare patch near water, nesting area of *C. capicola* and *C. lichtensteinii* on Hilton Farm, Eastern Cape, Nama-Karoo; b. nesting area of *C. toriger*, Skuinshoogte Pass, northeast of Nieuwoudtville; c. a nesting area of *C. damarinus*, near Omaruru, arid savanna, nesting aggregation sited in bare area at foot of termite heap. d. part of a nesting aggregation of *C. lichtensteinii*.



The number of nests encountered in any particular year and nesting area relates to conditions not only of that season but to those of previous years. After a succession of 'good' years, populations of *Ceramius* may be very large, for example in some years *C. nigripennis* has been found nesting in thousands along a river slope in the Goegap Reserve, Springbok, Namaqualand, from the river bank to the upper limit of the slope. Similarly, at Kransvlei in the hills to the southwest of Clanwilliam, *C. socius* has been found nesting in extremely large numbers in artificially created bare areas associated with a farm dam.



FIGURE 41. *Ceramius* nest entrance turrets: a. nest entrance turret of *C. metanotalis*; b. *C. damarinus* preparing to enter nest entrance turret; c. *C. lichtensteinii* with mud pellet at nest entrance (actual length of wasp 19 mm); d. nest entrance turret of *C. jacoti*.

Description of the nests

All the known nests of *Ceramius* species consist of a multicellular subterranean burrow surmounted by a subvertical or curved tubular mud turret of the same diameter as the burrow opening (Figures 41–49). Each successive cell terminates a secondary shaft. The section of the secondary shaft between the cell and the main shaft is filled with soil and is sealed off from the main shaft with a thin mud plate. Within each excavated cell of all but Group 4 as represented by *C. damarinus* and Group 8, is a constructed mud cell sealed with a mud plug. The diameter of the cells is greatest towards the rounded end. The structure of the subterranean burrow differs between species groups but is constant within a group.

In the nests of Group 2A and B (Figure 44) the relatively long, slender main shaft descends subvertically and for the greater part of its length is of the same diameter as the burrow entrance. Near the lower end of the shaft there is a short wider section forming a 'bulb' below which the shaft continues with a diameter equal to that of the upper section of the shaft. The main shaft at its base turns outwards to form a short lateral shaft terminating in a cell that lies subhorizontally. Successive cells terminate secondary lateral shafts and all lie to one side of the shaft in a group. The nests of *C. micheneri* investigated were all at the first-cell stage and at that stage they resemble those of Groups 2A and B.

In the nests of Group 3 (Figure 45) the burrow consists of a short shaft, with the upper part of the same diameter as the entrance and the lower part of a diameter up to three times as great depending upon the number of cells present. From the basal 'bulb' extend very short subvertical secondary shafts, each terminating in a cell.

The nature of the nests of Group 4 (Figure 46) is known only from *C. damarinus*; the burrows of *C. beyeri* investigated were incomplete. The burrow of *C. damarinus* consists of a short to

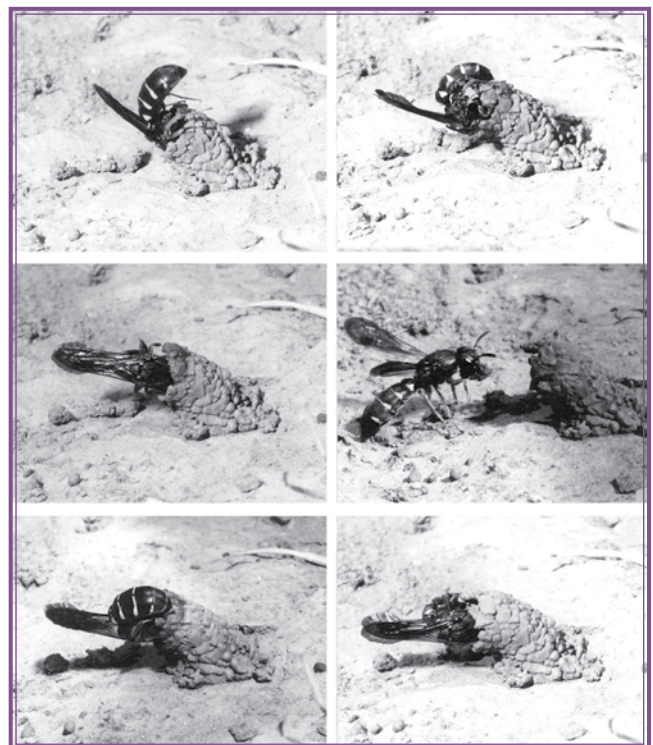


FIGURE 42. *Ceramius capicola* constructing nest entrance turret.

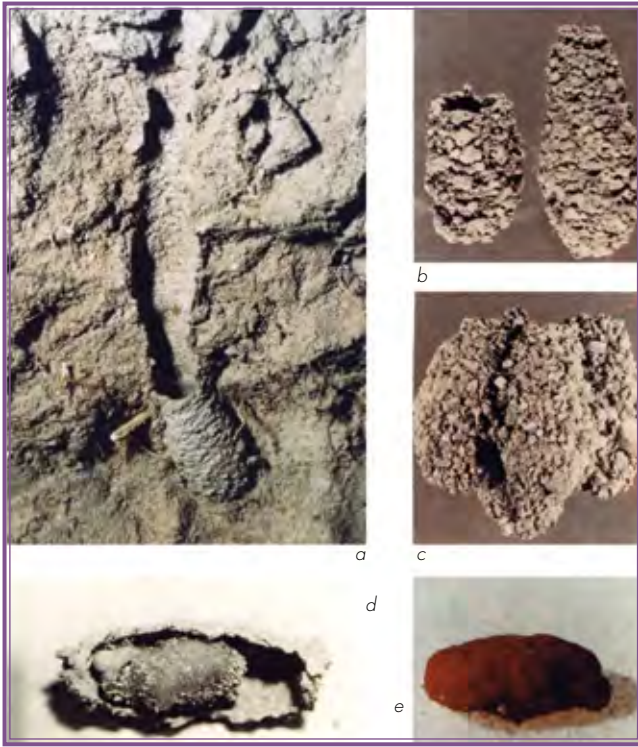


FIGURE 43a–e. a. vertical cutaway of newly constructed one-celled nest of *Ceramius jacoti*, showing bulb and constructed earthen cell; b. constructed earthen cells of *C. nigripennis*, half constructed (left) and completed (right); c. group of four completed and sealed earthen cells of *C. nigripennis*; d. constructed earthen cell of *C. cerceriformis*, cut longitudinally to show provision and position of young feeding larva; e. typical provision, a firm 'pollen loaf'.

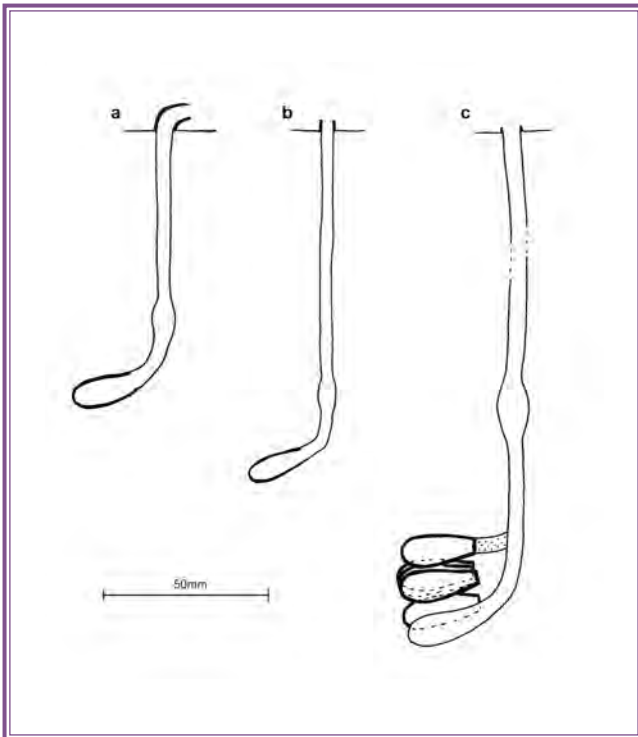


FIGURE 44. Vertical plans of nests of *Ceramius* Group 2 and of the closely allied *C. micheneri*: a. *C. cerceriformis*; b. *C. micheneri*; c. *C. clypeatus*. Nests are characterised by presence of turning 'bulb', cell terminating main shaft, cells subhorizontal and grouped to one side of the main shaft, and constructed cells within excavated cells.

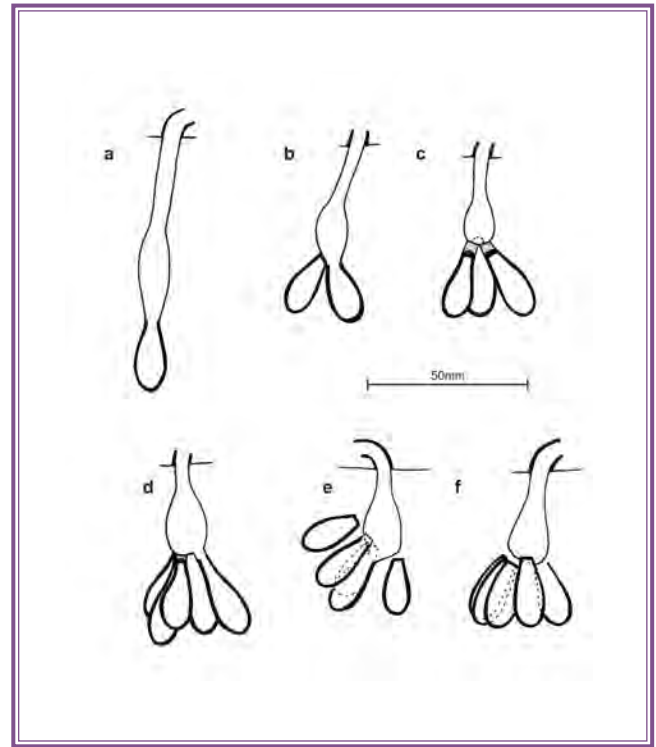
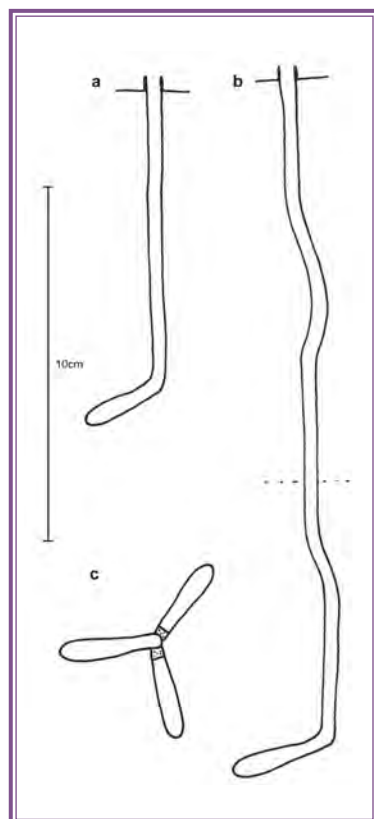


FIGURE 45. Vertical plans of nests of *Ceramius* Group 3: a. *C. jacoti*; b–d. *C. nigripennis*; e. *C. toriger*; f. *C. braunsi*. Nests are characterised by presence of turning 'bulb', cell terminating the main shaft, cells subvertical, grouped beneath the basal 'bulb', and constructed cells within excavated cells.

relatively long slender shaft of even diameter along its entire length, that is without a 'bulb'. The cells terminate short lateral shafts that radiate out from the base of the shaft in a single whorl.

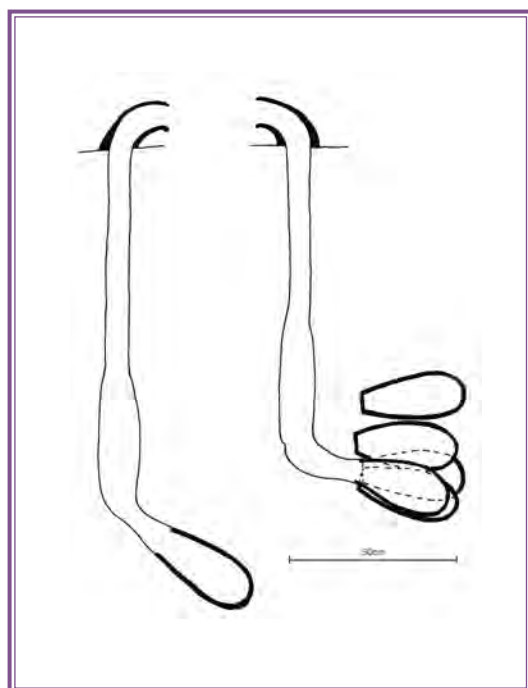
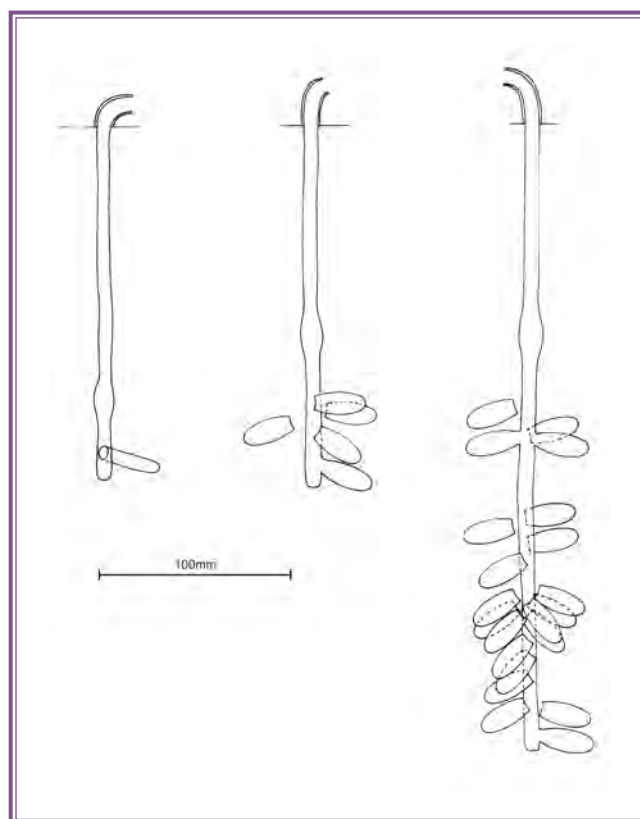
In the nest of the monospecific Group 5 (Figure 47) the relatively long main shaft descends subvertically. For the first third of its length it is of the same diameter as the burrow entrance. Then follows a short wider section forming a 'bulb' below which the shaft continues with a diameter equal to that of the upper section of the shaft. No cell terminates the main shaft. Extremely short, horizontal, lateral secondary shafts roughly grouped in whorls radiate out from the main shaft at depths from shortly below the 'bulb' to a short distance above the base of the main shaft.

In the nests of Group 6 (Figure 48), based on the nesting of two of the three species, the main shaft is of moderate length, descends subvertically and is initially of the same diameter as the entrance but widens after some distance. The wider section of the main shaft varies in length from nest to nest. In some new nests with only one cell the wide section is no more than a 'bulb' below which the shaft continues with a diameter equal to that of the upper section of the shaft. In nests at a more advanced stage, that is having several cells, the entire lower section of the subvertical shaft is wide. In some nests the diameter of this lower wide section of the shaft fluctuates so that its sides are very uneven. At the base of the subvertical section the shaft curves outwards to terminate in a cell that lies subhorizontally. Subhorizontal secondary shafts, each terminating in a cell, fan out from the main shaft but never form a complete whorl so that the cells lie together in a group. In some instances the cells are at different depths but always form a group.

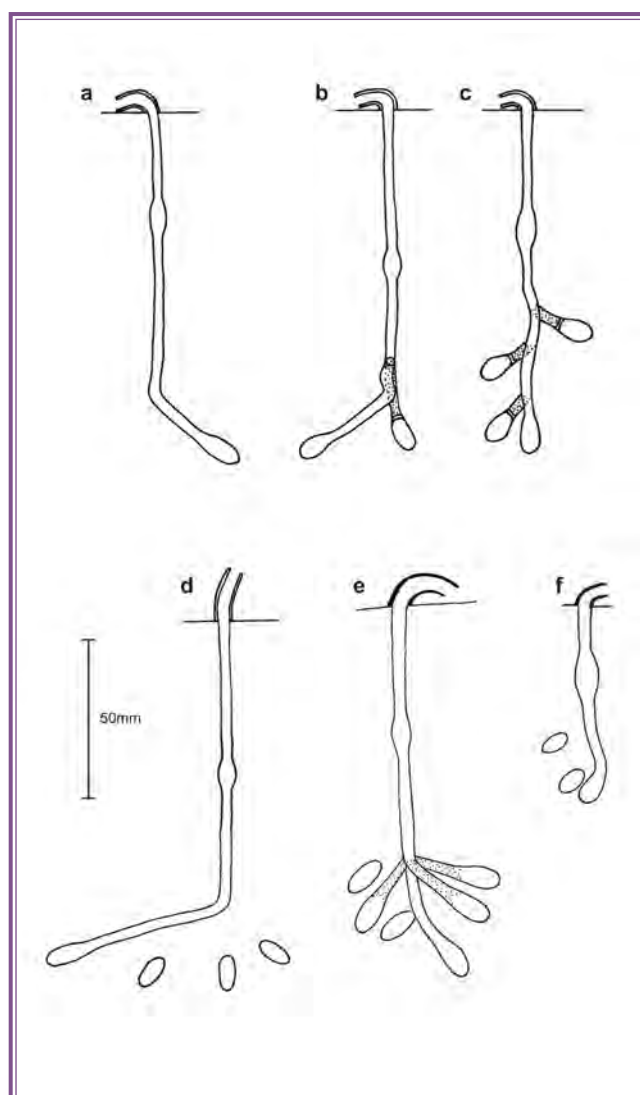


Left: FIGURE 46. Plans of nests of *Ceramius damarinus*, *Ceramius* Group 4: a and b. vertical plans; c. transverse plan. Nests characterised by lack of turning 'bulb', cell terminating the main shaft, cells subhorizontal, not grouped to one side of shaft, and no constructed cells within excavated cells.

Right: FIGURE 47. Vertical plans of *Ceramius* Group 5: *C. lichtensteinii*. Nests are characterised by presence of turning 'bulb', lack of cell terminating the main shaft, cells horizontal, not grouped to one side of shaft, and constructed cells within excavated cells.



Above: FIGURE 48. Vertical plans of nests of *Ceramius* Group 6: *C. rex*. Nests are characterised by presence of turning 'bulb', cell terminating main shaft, cells subhorizontal, grouped to one side of shaft, and constructed cells within excavated cells.



Right: FIGURE 49. Vertical plans of nests of *Ceramius* Group 8: a–c. *C. capicola*; d. *C. linearis*; e. *C. socius*; f. *C. bicolor*. Nests are characterised by presence of turning 'bulb', cell terminating the main shaft, cells sloping, not grouped to one side of main shaft, and no constructed cells within excavated cells.

In the nests of Group 8 (Figure 49), based on all four species, the relatively long main shaft descends subvertically and is of the same diameter as the entrance, with usually at approximately half its depth, a short 'bulb'. Towards its lower end the main shaft curves to one side and terminates in a sloping cell. Relatively long secondary shafts diverge from the main shaft at the level at which it departs from the subvertical. Each secondary shaft ends in a cell. An excavated cell is smoothed on the inside. Mud cells are not constructed. A completed cell is sealed with a mud plate.

Key to the southern African species groups based of differences in the architecture of the burrows:

- 1 Excavated cells not containing constructed cells 2
Excavated cells containing constructed cells 3
- 2 'Bulb' present in vertical shaft Group 8
'Bulb' absent Group 4
- 3 No cell terminating the main shaft Group 5
Cell terminating main shaft 4
- 4 Cells subvertical Group 3
Cells subhorizontal 5
- 5 'Bulb' short, bottom end well above level of cells Group 2
'Bulb' long, bottom end level with cells Group 6

Method of construction of the nest

All species of *Ceramius* in southern Africa visit water and all use water as a bonding agent in the construction of nest entrance turrets and 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 owing to the female's rotating evenly and 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.

Shaft diameter is in almost direct proportion to head width. Head width (measured across the eyes) ranges from 2.5–2.8 mm (*C. bicolor*) to 4.6–5.3 mm (*C. rex*) and shaft diameters range from 3.5–4.0 mm (*C. bicolor*) to 5.5–7.0 mm (*C. rex*). The variation in shaft diameter within a species is similarly explained by the variation in head width in individuals. This is nicely illustrated by the finding that nesting *C. lichtensteinii* at Hilton in the eastern Karoo had an average female head width (measured across the eyes) of 5.03 mm ($n = 30$, range 5.0–5.5 mm) and average shaft diameter of 6.2 mm ($n = 19$), whereas at Tierberg in the southern Great Karoo where average female head width was 6.35 mm ($n = 30$, range 6.0–7.0 mm) shaft diameter was 8.0 mm ($n = 22$). In other words, the head width of the Tierberg population was 26% greater than that of the Hilton population and shaft diameter was 29% greater.

The method of placement of pellets by *C. capicola* was the one most clearly observed. The wasp backs up the shaft with a pellet between her mandibles and, reaching the turret opening, holds the sides of the turret with her legs while placing the pellet in position and smoothing it on the inner surface with her mouth-parts and supporting it on the outer surface with the tip of the ventral surface of her abdomen, which is curved around for this purpose. As many as twelve pellets may be added to the turret per water load. If the turret is destroyed by rain or mechanical means, the wasp will build a new one of similar design and dimensions as the original one.

In the construction of a vertical cylindrical turret, pellets are added regularly (Figure 41c), whereas in a sloping or curved turret more pellets are added to the part of the turret wall that will be uppermost than to the part that will be lowermost (Figure 42).

The turret having been completed, the wasp continues to excavate the shaft but the pellets then extracted are discarded either in a definite pellet-dropping area in close proximity (Figure 41a) to the nest or at some distance. *C. metanotalis* and *C. capicola* are examples of species that have a clearly defined pellet-dropping area. When discarding a pellet, a female of *C. capicola* backs out from her nest until her head is free from her turret, then flies sideways and slightly forwards just above the surface of the ground to the pellet-dropping area a few centimetres from and to one side of the turret. She drops the pellet and, still orientated parallel to her turret, flies in reverse motion back to the nest entrance, which she is then facing, and enters. In this way the pellet-dropping operation takes up the minimum of time and exertion, differing from that of most mud-excavating wasps, including some species of *Ceramius* that fly up in a wide circle when dropping pellets. 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 in different localities. The nesting aggregations of one population were littered with discarded pellets whereas those of another were 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 head first. Cycles of water carriage and pellet extraction are performed rapidly and without interruption during active nest excavation.

Cell excavation having been completed and after a variable amount of smoothing and cementing of the cell surface, the cells of the Group 4 and Group 8 species are ready for oviposition whereas in the other groups a mud cell is first constructed within each excavated cell (Figure 43). Mud for the construction of these cells 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 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 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 has been 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 the nest. 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 dependent 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 the Group 3 plan does. *C. 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.

Re-use of nests

Re-use of nests seems to be the rule for wasps of Groups 3, 5 and 6, but no evidence has been found of re-use of nests by wasps of Groups 2, 4 and 8.

On emergence, wasps of Groups 3, 5 and 6 either initiate a new nest or enlarge the maternal nest. When several females emerge in a season, only one remains in the nest. All the others leave to initiate new nests. A re-used nest is surmounted by a newly constructed turret. A new cell is constructed or a vacated cell is cleaned out and re-used. In the case of a cell being re-used, the old cocoon is left in position. It seems that only the cell from which the possessor of the nest emerged is re-used; all other cells and secondary shafts leading to them are freshly excavated. A nest may be re-used over a period of several years.

Provision

The provision, a pollen and nectar mixture, is in the form of a firm pollen loaf (Figure 43e) 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 the provision of all species investigated was examined microscopically and compared with the pollen of flowers found in the vicinity of the nesting area. It was found that the pollen for the provision of each species was derived from flowers of a single family or genus and furthermore that this was constant within a species group. Foraging records indicate that nectar and pollen are almost always derived from the same flowers.

Sleeping and sheltering

When nests are being worked upon, sleeping or sheltering in the nest by females at night or in inclement weather is common amongst the pollen wasps, including *Ceramius* species.

Male behaviour

Mating

Observations on pairing of 11 species of southern African *Ceramius* have been made. Although all the observations are incomplete, they do demonstrate considerable variations in



FIGURE 50. a. *Ceramius socius* pairing on wet sand at water's edge; b. *C. linearis* pairing on water surface; c. *C. damarinus* copulating on water surface; d. *C. clypeatus* pairing on *Aspalathus spinescens*.

behaviour. *C. cerceriformis* (Group 2A) males and females are present together at water and at flowers. Mounting of females by males in the field has been observed only on wet soil at the water's edge where females stand to imbibe water. However, males have been observed on several occasions at various sites perched on a twig overlooking known forage plants appearing to be waiting for females as they reacted to other visitors to the flowers. When mounting a female, a male grasps her and holds

her pronotum with his front legs. The pair then flies up and settles on a bush or other object where it is believed that actual copulation takes place. If a pair collected at the water's edge is placed in a glass vial, the male mounts the female and copulates with her, making detailed observations possible.

Ceramius clypeatus (Group 2B) males and females are commonly present at flowers, but males have not been observed at water or in the nesting areas. Several instances of a pairing on a forage plant have been observed (Figure 50a). Having mounted a female, the male grasps her with his front legs, his middle and hind legs being held stretched out and closely along his sides. The antennae of the male are directed forwards and downwards, touching the female's antennae which are similarly directed forwards and downwards. Actual copulation was not observed.

Ceramius mitcheneri (Group 2C) females and males are commonly present together at water and at forage flowers. Females imbibe water standing at the water's edge. If a female and male are captured at a water site and placed together in a glass vial, mounting and copulation take place.

Females and males of *C. nigripennis*, *C. toriger* and *C. braunsi* (Group 3) are commonly present together at water and at forage flowers. *C. toriger* and *C. nigripennis* have been observed in copulation on forage plants. Females of all three species collect water while standing on the water surface. Large numbers of male *C. toriger* were observed 'waiting' on raised ground a short distance from and overlooking water being visited by females, but no instances of pairing were witnessed.

Ceramius damarinus (Group 4) males and females are present together at water and flowers. Males patrol to and fro over the surface of water and over forage plants. However, interactions have been observed at water only. When collecting water, a female, alights on the water surface. At the height of mating activity, one or more males descend on a female as soon as she alights on the water surface. She either resists the male's advances and flies off or accepts him. If he is accepted, he grasps her with his front legs and with his head positioned posterior to hers, extends his gaster so that the tip reaches the tip of her gaster, which he pulls upwards towards him while pressing the anterior ventral surface of his gaster, with processes on sternum 3, against the dorsal surface of her gaster at midlength. He then inserts his genitalia. The antennae of both are held up and away from the head. While copulation is taking place, the two usually momentarily lie together on their sides on the surface of the water (Figure 50b) before flying off together, the male above the female. In flight, the male releases his hold on the female with his front legs but his genitalia remain engaged. On hot, sunny days at the height of mating activity copulations continue until late afternoon.

Ceramius lichtensteinii (Group 5) males and females are commonly present together at water, at flowers and in nests. Interactions have been observed at water and on forage flowers. Females collect water while standing on the surface of the water. Males patrol to and fro over the water. As a female arrives on the water, one or more males descend towards her. A female may accept a male or avoid him by flying off. If a male is accepted, he clasps the female's thorax and after a few seconds he flies off holding the female firmly beneath him. At this stage copulation has not occurred. It was not established when

or where actual copulation takes place. On several occasions males have been observed mounting females on flowers of *Sphalmanthus* cf. *bijliae* (Aizoaceae: Mesembryanthema). As the flowers are small, the female balances herself on the rim of the flower. Males mounting females were therefore positioned in this semivertical stance. It was not established whether actual copulation took place on the flowers.

Ceramius rex and *C. metanotalis* (Group 6) males and females are present together at water and at forage flowers (Asteraceae) but males have not been observed in association with nests. The females of both species imbibe water while standing on the water surface. Males of *C. rex* have been observed attempting to pair with females on water.

Males and females of *C. linearis*, *C. capicola*, *C. socius* and *C. bicolor* (Group 8) are all commonly present together at water and forage flowers. Males of *C. socius* and *C. bicolor* only have been observed in the nesting areas. Females of all but *C. socius* imbibe water while standing on the water surface. Males of *C. linearis* and *C. capicola* patrol to and fro over the water. When a female lands on the water surface, one or more males descend towards her. She may accept a male or avoid him by flying off. If a male is accepted, he clasps the female's thorax (Figure 50c) and after a few seconds flies off, holding her firmly beneath him. After a short flight, the pair alights on the ground and separates. The actual moment of copulation has not been established, but circumstantial evidence suggests that for both species this must be accomplished during flight. While working together with us, Annette Berger, a student of Volker Mauss, made detailed close observations. She established that as a male *C. linearis* lands on a female, his legs are spread out. He then clasps the female around the pronotum with his front legs. While he is positioning himself both male and female move their heads rapidly from side to side, with their antennae extended laterally. When the male is in position, his head is above that of the female and the posterior tip of the abdomen is above hers; the antennae of both are drawn back but are not touching; his wings are raised but hers are folded; and he holds her with all three pairs of legs with their tibiae firmly tucked beneath her, the tibia of the third pair being anterior to her gaster. As the pair flies off, the male releases his hold with all but his front legs, his second and third legs being stretched upwards and backwards, releasing the female's wings so that in flight both male and female wings are in operation. Although females of *C. bicolor* imbibe water while standing on the water surface, pairings take place on the wet soil at the water's edge.

In contrast to the other three species of *Ceramius*, Group 8, *C. socius*, does not imbibe water while standing on the water surface but from wet soil near the water's edge. Males are present in the nesting area in the early morning before the females emerge from their nests. However, at this time of day, at least, there appear to be no interactions between males and females. Females aggregate at a small, selected watering point. Shortly after their arrival they are joined by the males who descend upon them (Figure 50d). A male alights on a female, grasping her with his front legs just posterior to her pronotum. His middle and hind legs are drawn up and back. His wings, like those of the female, are folded over his back. After a short while the male flies off, grasping the female firmly. On warm, sunny days at the height of mating, pairings continue until late afternoon.



Nest guarding

Males of six species of *Ceramius*, *C. micheneri*, *C. toriger*, *C. lichtensteinii*, *C. capicola*, *C. socius* and *C. bicolor*, have been observed in association with nests. *C. socius* males are present in the nesting areas before the females emerge from their nests in the morning. After pairing with the females at their watering point they do not, however, seem to return to the nesting area and no males were found sheltering in nests. On the other hand, males of *C. bicolor* guard the nests while the females are away from them. Each nest seems to be attended by a male. The male guard drives off other males or any other insects that come too near the nest. On a cloudy day, when four nests were investigated, two contained a male each. These two nests each contained an unsealed but provisioned cell. Similarly, males of *C. lichtensteinii* (Figure 51) and *C. capicola* are present in the nesting area while nesting activities are in progress. We noted one instance of a male *C. micheneri* and two of a male *C. toriger* together with a female in her nest.



FIGURE 51. Male *Ceramius lichtensteinii* leaving a nest.

Associated organisms

Ectoparasites

Acarina, mites

Examination of all the southern African genera of masarines revealed an association of mites with *Ceramius* alone. The 2 232 individuals examined represented all 20 species of *Ceramius* in southern African. In this sample, mites were found on all species of Groups 3 and 6, all of which provision with composite pollen, but none were found on the species of Groups 4, 5 and 8, which provision with pollen from Aizoaceae. However, the division on the basis of flower family visited is not clear cut as the two species of Group 2A, both of which provision with mesemb pollen, bore mites. Similarly, the two species of Group 2B, both of which provision with papilionate pollen, bore mites but none were found on the closely allied *C. micheneri*, which also provisions with papilionate pollen.

Most species lack acaritaria, but a pair of acaritaria are present, positioned laterally, on the metanotum of *C. caffer*, *C. metanotalis* and *C. rex* (Figure 52b).

The mites were all hypopi (= heteromorphic deutonymphs) of the family Winterschmitiidae (= Saproglyphidae). A species of *Zethovidia* was obtained from adult females of Groups 2, 3

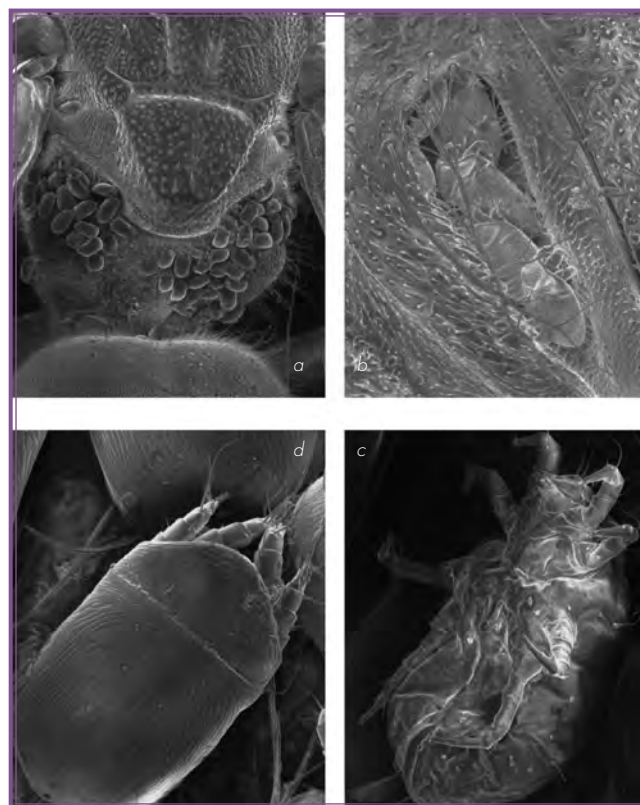


FIGURE 52. Acarina: a. hypopi of a winterschmitiid mite on an adult female *Ceramius nigripennis*; b. hypopi of a winterschmitiid mite in one of the pair of acaritaria of an adult female *C. rex*; c. and d. a winterschmitiid mite (actual length of mite $\pm$ 0.24 mm).

and 6 and a species of *Kennethiella* only from adult females of Group 3.

Endoparasites

Conopidae, thick-headed flies

Volker Mauss, during the course of a study of the internal morphology of *Ceramius*, dissected 23 females of *Ceramius linearis*. In the haemocoel of the metasoma of six specimens he found dipterous larvae, one in each of five and two in the sixth. Furthermore, in one male *Ceramius lichtensteinii* he found one dipterous larva in the haemocoel of the metasoma. All of these specimens were from a single locality. No *Ceramius* specimens from other localities contained dipterous larvae.

The larvae were all in early instars and firm identification was therefore not possible. However, Mauss is of the opinion that they were probably Conopidae (pers. comm.).

'Parasites' in nests

Mutillidae, velvet ants

Dasyabroides caffer Kohl (Figure 53) has been reared from cocoons of *C. lichtensteinii*. It is not, however, specific to pollen wasp hosts, having also been reared from cocoons of two sphecoid wasps, *Ammophila ferrugineipes* (Lepelletier) and *Ammophila insignis* F. Smith.

Chrysididae, cuckoo wasps

Three species of *Allocoelia* have been found in association with nests of *Ceramius*—*A. capensis* (F. Smith) (Figure 54) with *C. lichtensteinii* and *C. cerceriformis*, *A. latnota* Edney with





FIGURE 53. A pair of *Dasylabroides caffer* (Mutillidae), female on left, male on right. Actual length 8 mm.



FIGURE 54. *Allocoelia capensis* (Chrysididae: Allocoeliini). Actual length 12.5 mm.



FIGURE 55. *Ceroctis groendali* (Meloidae: Lyttinae: Mylabrini). Actual length 12 mm.

C. capicola and *C. lichtensteinii*, and *A. minor* Mocsáry with *C. capicola* and *C. clypeatus*.

Meloidae, blister beetles

Ceramius lichtensteinii is host to *Ceroctis groendali* (Billberg) (Lyttinae: Mylabrini) (Figure 55) 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 that wait in flowers for visiting bees.

Nest usurpers

Megachilidae, leaf cutter bees

We have recorded *Megachile aliceae* Cockerell from nests of *C. nigripennis* in the Springbok district, Namaqualand (Figures 56 and 57), and of *C. braunsi* in the Clanwilliam (Figure 58) district, Olifants River Valley, and an undetermined megachilid from nests of *C. jacoti* in the Oudtshoorn district, Little Karoo. *Megachile aliceae* is not restricted to usurping nests of masarines, having been recorded by us usurping nests of eumenines, *Parachilus insignis* (de Saussure) in the Grahamstown district, Eastern Cape, and *Paravespa mima* Giordani Soika in the Prince Albert district, southern Karoo.

It was the activity of *Megachile aliceae* that originally attracted our attention to the presence of a *C. nigripennis* nesting aggregation. Several of the bees were harassing these pollen wasps which had clearly just started nesting as all were constructing turrets. Three days later when 15 turreted nests were investigated, three contained bee cells. In two of the nests the bee had made use of the cell from which the wasp had emerged. It was clear that the pollen wasp had been evicted. The third nest was a newly excavated one with a single newly constructed mud cell in which the bee had constructed her own cell. In addition, two nests from which no *C. nigripennis* had emerged in the present season both contained cells of *M. aliceae*.



FIGURE 56. Nest of *Ceramius braunsi* usurped by *Megachile aliceae* (Megachilidae), showing a petal cell of the bee within a cell of the host.

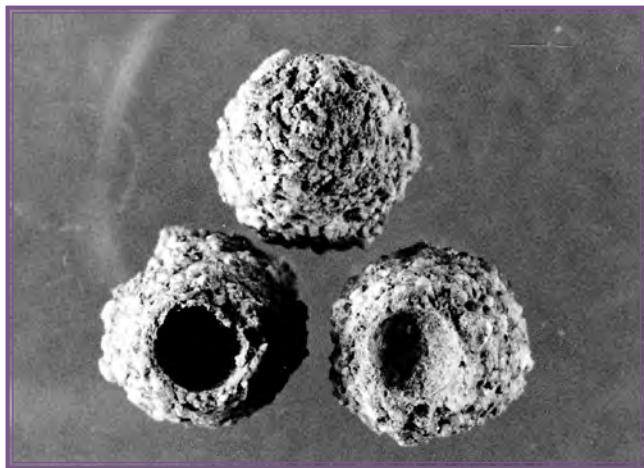


FIGURE 57. Three earthen cells of *Ceramius nigripennis*: convex seal of *C. nigripennis* (top); open cell (bottom left); concave seal of *Megachile aliceae* (Megachilidae) (bottom right).

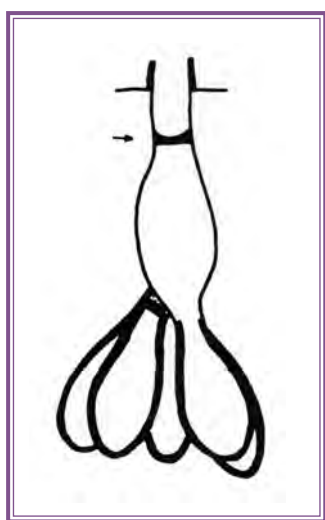


FIGURE 58. Vertical plan of nest of *Ceramius nigripennis* usurped by *Megachile aliceae* (Megachilidae), showing position of final bee seal (arrow).

Megachile aliceae constructs its flask-shaped petal-cell within the cell of the masarine in such a way that it entirely fills the latter. The petal-cells from *C. nigripennis* nests were all constructed from lengths cut from the orange 'petals' of the Namaqualand daisy, *Dimorphotheca sinuata* (Asteraceae), and three of those from *C. braunsi* nests from the pink petals of a species of *Pelargonium* (Geraniaceae) (Figure 56). The 'petal' pieces are carried to the nest cut-end first and are placed with the 'petals' running vertically and tucked under at the bottom. After provisioning and oviposition have taken place, the cell is sealed using shorter pieces of petal laid crosswise with the ends curved upwards into the mouth of the wasp's mud cell. The mud cell is then sealed with a mud plug that is concave above with the surface smoothed, readily distinguishable from that of *Ceramius*, which is convex and rough (Figure 57).

The bee constructs a final closure in the main shaft about 5 mm below the ground surface (Figure 58). 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.

The megachilid that had invaded a *C. jacoti* nest had constructed a leaf cell within the nest.

Currently recognised species

- C. beyeri* Brauns, 1903; Western and Eastern Cape
C. bicolor (Thunberg), 1815 (*Philanthus*); Western Cape
C. braunsi Turner, 1935; Western Cape
C. brevitaris Gess, 1997; Richtersveld, Northern Cape
C. caffer de Saussure, 1855; Western Cape
C. capicola Brauns, 1902; Eastern Cape
C. cerceriformis de Saussure, 1853; Western Cape and Namaqualand, Northern Cape
schulthessi Brauns, 1902
vespiformis de Saussure, 1855
C. clypeatus Richards, 1962; Western Cape
C. damarinus Turner, 1935; Namibia
C. jacoti Richards, 1962; Western Cape
C. lichtensteinii (Klug), 1810 (*Gnatho*); Western Cape and Eastern Cape
macrocephalus de Saussure, 1854
rufimaculatus Cameron, 1906
C. linearis Klug, 1824; Eastern Cape
fumipennis Brauns, 1902
C. metanotalis Richards, 1962; Western Cape
C. micheneri Gess, 1968; Western Cape
C. nigripennis de Saussure, 1854; Namaqualand, Northern Cape
hessei Turner, 1935
C. peringueyi Brauns, 1913; Western Cape
C. rex de Saussure, 1855; Namaqualand, Northern Cape
C. richardsi Gess, 1965, Western Cape
C. socius Turner, 1935; Western Cape
C. toriger von Schulthess, 1935; Western Cape and southwestern Northern Cape

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RICHARDS, O.W. 1962. *A revisionary study of the masarid wasps (Hymenoptera: Vespidae)*. British Museum (Natural History), London. 295 pp.



Masarina: *Jugurtia*

Jugurtia species are ± 7 –12 mm long, most species being shorter than ± 10 mm. The range in length overlaps that of *Masarina* (± 5 –9 mm), the most closely related genus, but to the practised eye they can be readily distinguished in the field, *Masarina* being more stockily built. Most are smaller than the majority of *Ceramius* (± 10 –20 mm long). The largest species, *J. elegans* (± 11 –12 mm long), is known only from the desert fringe in northern Namibia. It is readily distinguished from the only Namibian species of *Ceramius*, *C. damarinus*, which is ± 13 –15 mm long and strikingly different in coloration.

The antennal club is tapered towards the base as in all genera other than *Celonites* and *Quartinia*, in which the antennal club is rounded.

As in *Ceramius* and *Masarina*, the wings do not fold longitudinally like those of *Celonites* and *Quartinia*.



FIGURE 59. Pair of *Jugurtia confusa*, female on left (actual length ± 9 mm) and male on right.

Jugurtia is considered to be the genus most closely allied to *Masarina*. In *Jugurtia* there is a transverse furrow at the base of the second gastral sternum whereas this furrow is lacking in all species of *Masarina*. Both genera have a preoccipital carina that runs posteriorly across the vertex. In *Jugurtia*, however, the carina extends down the tempora whereas in *Masarina* it is effaced, the tempora being rounded, with at most a change in the sculpturing indicating the course taken by the carina in the former genus. *Jugurtia* is characterised by a marked sexual dimorphism, which is manifested in the males not only by the elongated and variously modified antennae, but also by the generally narrow abdomen and difference in coloration (Figure 59). *Masarina* exhibits very little sexual dimorphism, the males looking much like the females and requiring close scrutiny for separation (Figure 64).

Tongue length in *Jugurtia* is ± 4 –7 mm, with the ratio of tongue length to body length ± 0.4 –0.6.

Distribution

Jugurtia is found in both the Afrotropical Region, where the greatest species diversity is in southern Africa, and the Palearctic Region. No species are common to both zoogeographical

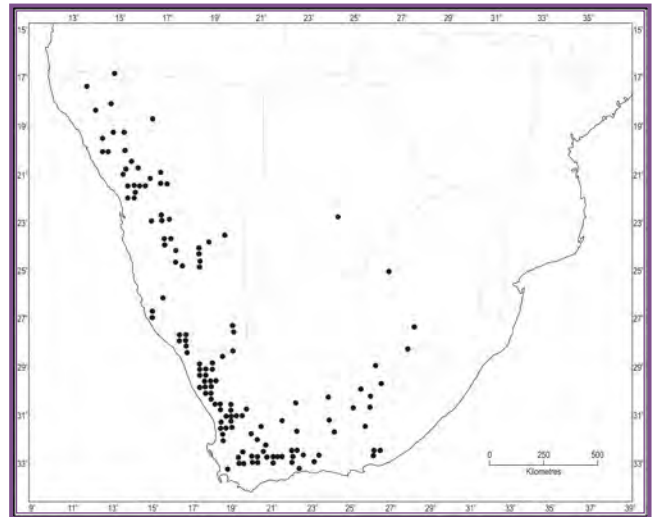


FIGURE 60. The known distribution of *Jugurtia* in southern Africa.

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 Little Karoo, the southwestern Fynbos, north through the Olifants River Valley, and from Namaqualand north to the Kunene River (Figure 60). Five species bridge the Orange River, 13 species have been found only south of the Orange 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 species (Appendix 2). Thirteen species, 76%, have been recorded from flowers of Asteraceae, flowers of which are known to be visited by a Palearctic species of *Jugurtia* as well. Of the 13, at least four species have been shown to have a strong association with Asteraceae—*J. braunsiella* in the Little Karoo, Robertson Karoo, Tankwa Karoo, Olifants River Valley and Namaqualand; *J. eburnea* in southeastern Namaqualand; *J. tibialis* in western Namibia from south to north; and *J. turneri* in the southern Tankwa Karoo. *Jugurtia braunsi* has been collected widely from Asteraceae but equally commonly from Aizoaceae: Mesembryanthema and less commonly from Campanulaceae and Scrophulariaceae. Four more species visit Asteraceae infrequently.

Considering the strong overall association of pollen wasps in southern Africa with Aizoaceae, it is of note that only four species, 24%, have been collected from this family. Of these, *J. nigrifrons* and *J. braunsi*, endemic to western South Africa, show a strong preference for mesembs throughout Namaqualand, but *J. braunsi* has also been recorded from four other families, most notably Asteraceae. In the southeastern Nama-Karoo *J. confusa* provisions its nest cells with mesemb pollen and has not been collected from flowers of other families, suggesting oligolecty, but west of Windhoek in Namibia it was found abundantly visiting *Hermannia* (formerly Sterculiaceae, now included in Malvaceae) although mesembs were present. For the fourth species, *J. calcarata*, there are only four flower-visiting records, three from mesembs and one from Asteraceae.

Three species show a strong association with *Hermannia* (Malvaceae)—*J. alfeni*, in the southeastern Nama-Karoo,

southern Kalahari, and southern and western Namibia through to the Kaokoveld; and *J. damara* and *J. mandibulata* in western Namibia from south to north. It therefore seems that *Hermannia* species are important forage plants for *Jugurtia* in some areas. *Hermannia* species are also important forage plants for some species of the closely related genus *Masarina*.

Two species, *J. namibicola* and *J. codoni*, are strongly associated with Boraginaceae. *Jugurtia namibicola*, restricted to the desert areas of northwestern Namibia, has been collected at diverse sites visiting solely *Heliotropium tubulosum* although a wide range of flowers was available at these sites. *Jugurtia codoni* appears to show a preference for *Codon* (formerly Hydrophyllaceae, now included in Boraginaceae) but also visits *Peliostomum* (Scrophulariaceae) and *Pelargonium* (Geraniaceae) and, in addition, has been recorded from four other families, probably as a casual visitor.

No species of *Jugurtia* have been found to specialise in visiting Scrophulariaceae. Two species, *J. koeroegabensis* 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*. *Ferraria* is also occasionally visited by *Celonites capensis*.

(See figures under 'Pollen wasps as flower visitors and potential pollinators'.)

In the Palaearctic, some species of *Jugurtia* have been recorded from Apiaceae (Umbelliferae). This is of interest as wasps and bees visiting Apiaceae in southern Africa are well collected but there are no records of visits by pollen wasps.

Water visiting

Females of 10 species of *Jugurtia*, *J. alfkeni*, *J. braunsi*, *J. braunsiella*, *J. confusa*, *J. damara*, *J. einensis*, *J. mandibulata*, *J. nigrifrons*, *J. polita* and *J. saussurei*, have been collected imbibing water from saturated soil near the edge of a water source (Figure 61).

Males were never observed at water.



FIGURE 61. Water collection, *Jugurtia braunsi*, females imbibing water from saturated soil at the water's edge.

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.

Nesting area and nest situation

Jugurtia confusa was found nesting to the northwest of Grahams-town (Figure 40a) in the Eastern Cape and *J. braunsi* in the Skuinshoogte Pass, northeast of Nieuwoudtville (Figure 40b).

The nests of both species were in bare areas in horizontal to sloping ground in 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.

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.

Description of the nest

Nests of *J. confusa* and *J. braunsi* consist of a subterranean burrow surmounted by a short cylindrical mud turret. The subterranean burrow consists of a vertical shaft of constant diameter for its entire length. From its lower end a short subhorizontal shaft branches off, terminating in an excavated cell within which is a constructed mud cell.

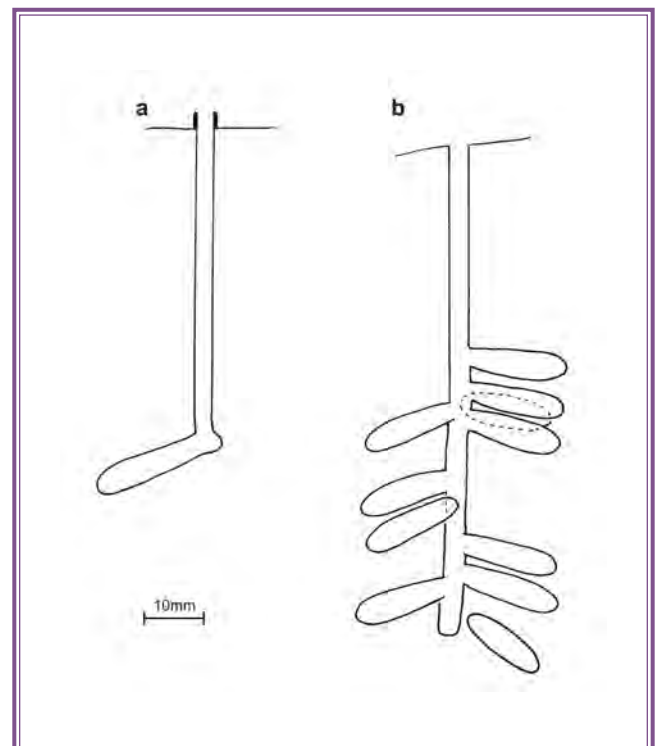


FIGURE 62. Vertical plans of turrets and underground workings of nests of *Jugurtia confusa*: a. newly constructed nest; b. re-used nest. Nest characterised by lack of cell terminating the main shaft, cells subhorizontal, not grouped to one side of the main shaft, and constructed cells within excavated cells.

Of the nests investigated, only one, a nest of *J. confusa*, was at a more advanced stage of construction. In this nest further subhorizontal secondary shafts, each terminating in a cell, were present (Figure 62). 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, like a cork in a bottle.

Method of construction of the nest

Jugurtia confusa and *J. braunsi* use water as bonding agent. 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*. This may well account for the penetration of the desert by at least two species, *J. gariensis* in the south and *J. namibicola* in the north.

Nest excavation by *J. confusa* and *J. braunsi* 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 makes a pellet. From each cropful of water a number of pellets are formed this way. The first pellets excavated from the shaft-initial may be discarded. The shaft-initial is circular in cross section due to the female's rotating evenly, not altering the direction of rotation without first completing a circle. At the commencement of turret construction, the pellets, instead of being discarded, are laid down in a circle around the shaft-initial in such a way that the inner diameter of the turret will be the same as that of the shaft (Figure 63). Additional pellets are added regularly so that the resultant turret is a vertical cylinder.

After completion of the turret, the wasp continues to excavate the shaft but the pellets then extracted are discarded. *J. confusa* has no clearly defined pellet-dropping area, but the wasp does confine her arrivals at and departures from the nest to a set quarter segment.

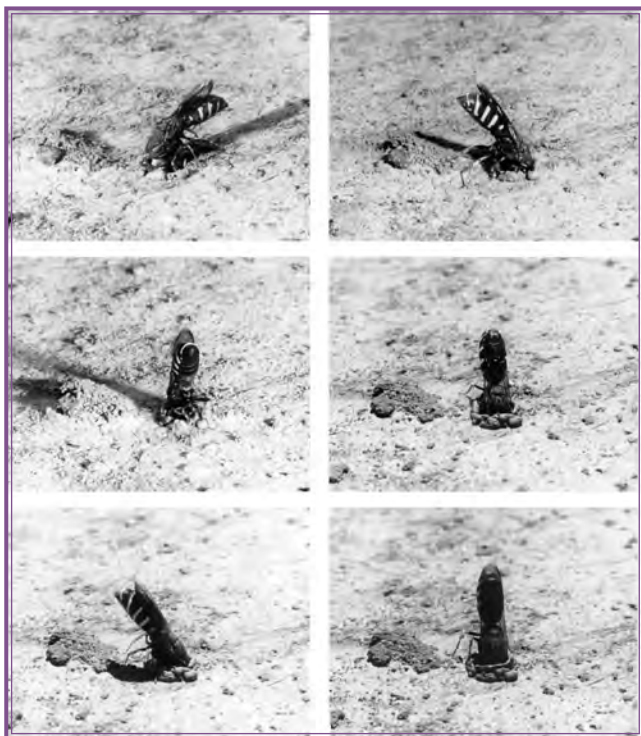


FIGURE 63. *Jugurtia confusa* extracting mud from shaft-initial and using the extracted pellets to construct an entrance turret, turret in early stage of construction.

Cycles of water carriage and pellet extraction are performed rapidly and without interruption during active nest excavation. Shaft diameter is maintained constant so that there is no 'turning bulb' as formed by *Ceramius*. Consequently the wasp continues to emerge backwards throughout shaft excavation.

From the bottom of the main shaft a secondary shaft is excavated in a subhorizontal 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 probable that at least part of the soil used in constructing the mud cell is excavated from this source. 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. The average thickness of the walls is 0.7 mm.

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 are constructed in the same manner, the number probably being dependent on the availability of water for nest construction and on pollen and nectar for cell provisioning.

Re-use of nests

Evidence for re-use of nests by *J. confusa* has been found. A nest marked at the end of one summer season was being worked upon by a freshly emerged female which had furnished it with a new turret at the start of the following season. Sunning himself in the vicinity of the nest was a freshly emerged male. It was found that eleven cells were open, empty and parchment-lined. They were therefore clearly cells from a previous year's nesting season.

Provision

The provision of *J. confusa*, the only species of *Jugurtia* for which provision has been obtained, is a moist sticky loaf composed of pollen and nectar. Pollen from the provision was examined microscopically and compared with pollen from flowers found in the vicinity of the nesting area. It was all of one type and matched that of *Drosanthemum parvifolium* (Aizoaceae: Mesembryanthema). As *J. confusa*, west of Windhoek, was collected abundantly but only from *Hermannia comosa* (Malvaceae), it is possible that provision may not be derived from Mesembryanthema throughout the range of the species.

Available flower-visiting records indicate that the provision of *J. braunsi*, *J. discrepans*, *J. eburnea*, *J. tibialis* and *J. turneri* is most probably derived from flowers of Asteraceae, that of *J. nigrifrons* most probably from Asteraceae and Mesembryanthema, that of *J. alfeni*, *J. damara* and *J. mandibulata* most probably from *Hermannia* (Malvaceae) and that of *J. namibicola* most probably from *Heliotropium tubulosum* (Boraginaceae). Provision of *J. braunsi*, *J. codoni* and *J. koeroegabensis* is of uncertain provenance but most probably mixed as each of these wasps have been found visiting flowers of several families.

Sleeping and sheltering

When nests are being worked upon, sleeping or sheltering in the nest by females at night or in inclement weather is practised by *Jugurtia confusa*.

Male behaviour

Jugurtia males and females are present together at forage flowers and *J. confusa*, at least, in the nesting area. Although 10 species of *Jugurtia* have been collected and observed at water, males have not been collected or sighted at water. *Jugurtia confusa* males have been observed to fly low, 5–8 cm above the ground, particularly skirting bushes at the periphery of the nesting area and also alighting on the ground in the vicinity of the nesting area from where they rise up to chase females and each other. They were seen to descend rapidly on females and although copulation was not observed, it seems likely that it takes place within the vicinity of the nesting area.

Associated organisms

Nest 'parasites'

Chrysididae, cuckoo wasps

The only cuckoo wasp found in association with *Jugurtia* is *Spintharina bispinosa* Mocsáry, which was found in a nesting aggregation of *J. confusa*, but it was not reared from nests. The only rearing of this species was from nests of *Celonites andrei*.

Currently recognised species

- J. affkeni* du Buysson, 1904 (Masaris); Kalahari, Botswana and Namibia, and Western Cape
- J. braunsi* (von Schulthess), 1929 (*Ceramiellus*); Western Cape, Namaqualand, Northern Cape
- J. braunsiella* (von Schulthess), 1930 (Masaris); Western Cape, Eastern Cape, Northern Cape and Namibia
- J. calcarata* Richards, 1962; Western Cape and Northern Cape
- J. codoni* Gess, 1997; Namaqualand, Northern Cape
- J. confusa* Richards, 1962; Western Cape, Eastern Cape, Northwest Province, Free State and Namibia
- J. damara* Gess, 2004; Namibia and Angola
- J. discrepans* (Brauns), 1913 (Masaris); Western Cape, Eastern Cape, Northern Cape and Namibia
- J. duplicata* Richards, 1962; Western Cape and Northern Cape
- J. eburnea* (Turner), 1935; Western Cape, Eastern Cape and Northern Cape
- polita* Richards, 1962
- J. einensis* Gess, 2004; Northern Cape
- J. elegans* Gess, 2004; Namibia
- J. gariensis* Gess, 2004; Richtersveld, Northern Cape
- J. hessei* Gess, 2004; Eastern Cape

J. koeroegabensis Gess, 1997; Richtersveld, Northern Cape and Namibia

J. mandibulata Gess, 2004; Namibia

J. namibicola Gess, 2004; Namibia

J. nigrifrons Gess, 2004; Western Cape and Northern Cape

J. saussurei (Brauns), 1905 (Masaris); Western Cape, Eastern Cape and Northern Cape

J. spinolae (de Saussure), 1855 (Masaris); no locality given

J. tibialis Gess, 2004; Namibia

J. tigrina Gess, 1997; Western Cape and Northern Cape

J. turneri (von Schulthess), 1929 (*Masariella* ?); Western Cape and Northern Cape

J. zebra Gess, 2004; Western Cape

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RICHARDS, O.W. 1962. *A revisionary study of the masarid wasps (Hymenoptera: Vespoidea)*. British Museum (Natural History), London. 295 pp.



Masarina: *Masarina*

Masarina is considered to be the genus most closely allied to *Jugurtia*. The range in length of ± 5 –9 mm overlaps that of *Jugurtia* (± 7 –12 mm), but to the practised eye individuals of *Masarina* are readily distinguishable in the field, being more stockily built. In *Masarina* there is no transverse furrow at the base of the second gastral sternum as is present in all species of *Jugurtia*. Both genera have a preoccipital carina that runs posteriorly across the vertex. In *Jugurtia*, however, the carina extends down the tempora whereas in *Masarina* it is effaced, the tempora being rounded, with at most a change in the sculpturing indicating the course taken by the carina in the former genus. *Masarina* exhibits very little sexual dimorphism, the males looking very like the females and requiring close scrutiny for separation (Figure 64). *Jugurtia* is characterised by a marked sexual dimorphism manifested in the males not only by the elongated and variously modified antennae but also by the generally narrow abdomen.

The antennal club is tapered towards the base as in all genera other than *Celonites* and *Quartinia* in which the antennal club is rounded.

As in *Ceramius* and *Jugurtia*, the wings do not fold longitudinally like those of *Celonites* and *Quartinia*.

Tongue length in *Masarina* is ± 3 –7 mm, with the ratio of tongue length to body length ± 0.4 –0.8.



FIGURE 64. Pair of *Masarina familiaris*, female on left (actual length ± 9 mm), male on right.

Distribution

Masarina is endemic to and restricted to southern Africa. 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 (Figure 65). Within the area of distribution of the genus some species, for example *M. strucki* and *M. familiaris*, associated with *Hermannia* (Malvaceae) and Cape Crotalariaeae (Fabaceae: Papilionoideae), are relatively widely distributed having being found from Namaqualand south to the Olifants River Valley and east

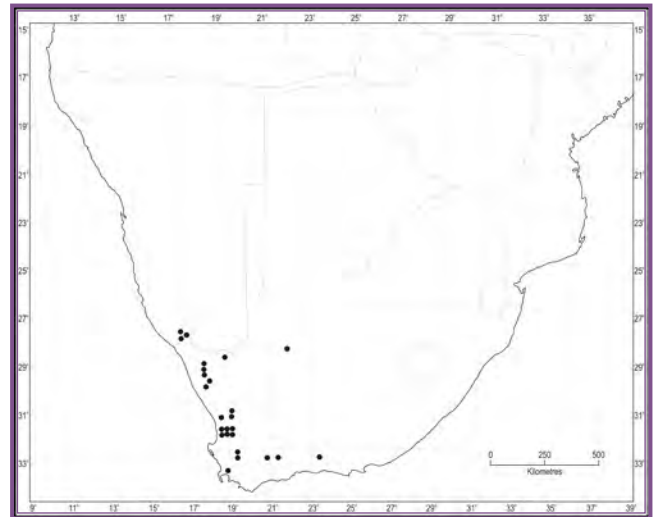


FIGURE 65. The known distribution of *Masarina* in southern Africa.

from there in the western Little Karoo and the southern Tankwa Karoo respectively. The most narrowly endemic species known is *M. tylecodoni*, which is restricted to the Richtersveld where it is associated with an equally narrowly endemic plant, *Tylecodon hallii* (Crassulaceae), 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 known species of the southern African genus *Masarina* (Appendix 2). Of these, 10 appear to be specialists. Three species, 23%, have been recorded solely from Papilionoideae (Fabaceae)—*M. ceres*, Gydo Pass; *M. familiaris*, Gydo Pass, Olifants River Valley and to the west, southeastern Namaqualand and Klipkoppe Namaqualand; and *M. hyalinipennis*, west of Olifants River Valley and Klipkoppe, Namaqualand. In addition, provision from the nests of *M. familiaris* was derived solely from *Aspalathus* (Papilionoideae).

Four species, 31%, have been recorded from *Wahlenbergia* (Campanulaceae). Of these, *M. parvula* and *M. namaqua*, known only from Klipkoppe Namaqualand, have been recorded solely from *Wahlenbergia* to date, but *M. mixta* and *M. mixtoides*, known from Namaqualand and the Olifants River Valley, have been frequently recorded from other flowers as well. The former has been collected from *Wahlenbergia* species but occasionally also from *Aspalathus* (Papilionoideae), *Hermannia* (Malvaceae), *Peliostomum* (Scrophulariaceae) and *Athanasia* (Asteraceae). Most records for *M. mixtoides* are from the northern Richtersveld from *Pelargonium klinghardtense* (Geraniaceae), a species also visited by *Jugurtia codoni*, but in this area it has in addition been collected from Asteraceae and Zygophyllum (Zygophyllaceae).

Three species, 23%, have been recorded from Aptosimeae (Scrophulariaceae). Of these, *Masarina peliostomi* in the Richtersveld and *M. aptosimi* near Groblershoop show a strong association and have been recorded solely from these flowers.

Two species, 15%, have been collected solely from *Hermannia* (Malvaceae formerly as Sterculiaceae)—*M. strucki*, western Little Karoo, Olifants River Valley and Klipkoppe, Namaqualand, and *M. hermanniae*, Aggeneys, Bushmanland.

Masarina tylecodoni, known only from the Richtersveld, forages in large numbers on *Tylecodon hallii* (Crassulaceae), endemic to and restricted to a relatively small area in northern Richtersveld and the northern extension of the Richtersveld, north of the Orange River. Although other 'pollen wasp flowers' are found flowering simultaneously, none have been found to be visited by *M. tylecodoni*, suggesting that this species is monolectic.

No species of *Masarina* have been recorded from Aizoaceae to date.

(See figures under 'Pollen wasps as flower visitors and potential pollinators.')

Water visiting

Of the 13 species of *Masarina* only two, *M. familiaris* and *M. hyalinipennis*, have been observed at water.

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*.

Description of nesting areas and 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 (Figure 66). The soil of the nesting sites varied from a sand-coloured clay-sand mixture with a relatively low proportion of clay to a hard nonfriable 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 also grouped in the vicinity of an old nest, suggesting that there is a tendency for a newly emerged female to initiate a nest in close proximity to the nest from which she herself emerged.

The nest of *Masarina strucki*, situated between two stones, was found in the Kamiesberg in a patch of *Hermannia disermifolia* bushes growing, characteristically for that area, in the lee of a large boulder (Figure 67). The soil was sandy and friable.



FIGURE 66. Nesting site of *Masarina familiaris* west of the Olifants River Valley.



FIGURE 67. Nesting site of *Masarina strucki* in the Kamiesberg, Namaqualand.

Description of the nest

The nest of *M. familiaris* consists of a multicellular burrow with a downwardly curved tubular mud turret at its entrance (Figure 68). The turret is constructed of mud pellets smoothed on the inside but left rough on the outside. A 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 are one or more subhorizontal to upwardly or downwardly sloping shafts, each ending in a cell (Figure 69). All shafts leading to sealed cells are filled with earth and sealed with a mud plate a short distance inside the burrow entrance. Over most of its length a cell is 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 truncate end wall.

The single nest of *M. strucki* consisted of a sloping burrow terminating in a cell (Figure 70). The cell, unlike that of *M. familiaris* but typical of most other *Masarinae*, was rounded at the inner end. There was no entrance turret (Figure 71). The seal was concave on the outside and convex on the inside.

Method of construction of the nest

Females of *M. familiaris* collect water for nest construction from saturated soil at the edge of a water source, but not all species



FIGURE 68. *Masarina familiaris* at nest entrance turret.

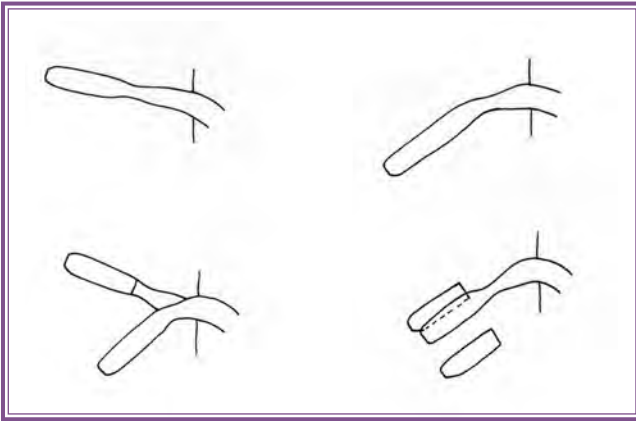


FIGURE 69. Vertical plans of turrets and underground workings of *Masarina familiaris*.

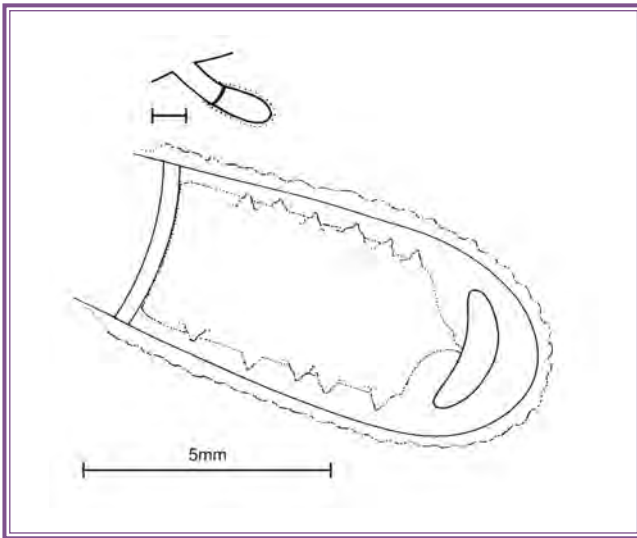


FIGURE 70. Vertical plans of nest and cell, papillate provision and egg of *Masarina strucki*.



FIGURE 71. *Masarina strucki* entering nest.

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.

The shafts are short and generally slope downwards, although they less commonly slope upwards (in a sample of 15, 13 sloped downwards and 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 has been created, the diameter returns to that of the shaft until the inner end of the cell is approached so that 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 truncate, not curved.

Although a mud cell is not constructed within it, the excavated cell is very carefully smoothed and shaped so that its walls are stabilised to such a degree that in nests constructed in relatively friable soils, at least 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 when 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 the use of 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 could be seen 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. Sealing of the cell had not been completed at the end of the day's work, at 17:07. The builder slept in the nest, with her head facing out and blocking the entrance until 10:37 the next morning. At 10:56 she left the nest and returned 13 minutes later to continue with closure of the cell. The seal was completed by 11:30.

Re-use of nests

No indication of re-use of nests has been found.

Provision

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. The provision of *M. strucki*, however, is jelly-like, pale ochre-yellow and translucent. It is addressed to the cell closure, but along its longitudinal surface it 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 (Figure 72).

In the Clanwilliam district, pollen used for provisioning by *M. familiaris* was derived solely from flowers of one or more *Aspalathus* species (Papilionoideae), 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 Crotalariaeae, 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* also obtains its provision from Cape Crotalariaeae and that *M. ceres* possibly does likewise.



FIGURE 72. Cell of *Masarina strucki* opened to show papillate provision and egg.

The pollen from the provision of *M. strucki* was all of one kind and matched that of *Hermannia disermifolia*. In other areas, pollen from other species of *Hermannia* would undoubtedly be used. Judging from foraging records, a second species, *M. hermanniae*, 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), that of *M. peliostomi* and *M. aptosimi* from Aptosimeae (Scrophulariaceae) and that of *M. mixta* from *Wahlenbergia* (Campanulaceae). Although foraging records suggest that most species are oligolectic, they show that *M. mixtoides* may well obtain its provision from more than one family of plants.

Provisioning of a single cell by *M. strucki* took 85 minutes and was apparently accomplished with five loads. During this phase the wasp was away from the nest, apparently foraging, for five periods varying from 6–10 minutes and rotated in the nest (an average of four times), apparently depositing the provision, for five periods of 3.0–13.5 minutes.

Sleeping and sheltering

When nests are being worked upon, sleeping or sheltering in the nest by females at night was observed for *M. familiaris* and *M. strucki*. Male *M. mixta* commonly sleep in the flowers of *Wahlenbergia* to which they and the females come to forage.

Male behaviour

Male and female *Masarina* of all species are present together at forage flowers. No instances of pairing have been observed. However, before the female emerged from her nest on the second day of a single nesting study on *M. strucki*, a male was seen in the vicinity of the nest resting on the ground and sunning himself.

Associated organisms

Nest 'parasites'

Chrysididae, cuckoo wasps

Allocoelia quinquedens Edney is probably 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 *M. familiaris* (Figure 73).

Nest usurpers

Megachilidae, leafcutter bees

Two nests of *M. familiaris* investigated were being attended by a leafcutter bee, *Hoplitis* sp. One nest was an old one, 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* species (Iridaceae) that was growing in the vicinity. After a petal cell had been sealed with pieces of petal, the excavated cell was sealed with compacted soil.



FIGURE 73. *Allocoelia glabra* (Chrysididae) at entrance to nest of *Masarina familiaris*.

Currently recognised species

- M. aptosimi* Gess, 2005; Northern Cape
- M. ceres* Gess, 1997; Western Cape
- M. familiaris* Richards, 1962; Eastern Cape, Western Cape and Northern Cape
- M. hermanniae* Gess, 2005; Northern Cape
- M. hyalinipennis* Richards, 1962; Western Cape and Northern Cape
- M. mixta* Richards, 1962; Western Cape and Northern Cape
- M. mixtoides* Gess, 1997; Richtersveld, Northern Cape
- M. namaqua* Gess, 1997; Northern Cape
- M. parvula* Gess, 1997; Northern Cape
- M. peliostomi* Gess, 1997; Richtersveld, Northern Cape
- M. roberti* Gess, 2005; Namibia
- M. strucki* Gess, 1988; Western Cape and Northern Cape
- M. tylecodoni* Gess, 1997; Richtersveld, Northern Cape

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- GESS, S.K. & GESS, F.W. 2004. Distributions of flower associations of pollen wasps (Vespidae: Masarinae) in southern Africa. *Journal of Arid Environments* 57: 17–44.
- GESS, S.K. & GESS, F.W. 2004. The distributions of the genera of the pollen wasps (Hymenoptera: Vespidae: Masarinae) in the semi-arid to arid areas of southern Africa in relation to their requirements for successful nesting. *Transactions of the Royal Society of South Africa* 59: 23–27.

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GESS, S.K., GESS, F.W. & GESS, R.W. 1997. Update on the flower associations of southern African Masarinae with notes on the nesting of *Masarina strucki* Gess and *Celonites gariepensis* Gess (Hymenoptera: Vespidae: Masarinae). *Journal of Hymenoptera Research* 6: 75–91.

Publications useful for identification of species

- GESS, F.W. 1997. Contributions to the knowledge of the species of the genera *Ceramius* Latreille, *Celonites* Latreille, *Jugurtia* de Saussure and *Masarina* Richards (Hymenoptera: Vespidae: Masarinae) in southern Africa. *Journal of Hymenoptera Research* 6: 36–74.
- GESS, F.W. 2005. Three new species of *Masarina* Richards, 1962 from southern Africa with a key to all species of the genus (Hymenoptera: Vespidae, Masarinae). *Journal of Hymenoptera Research* 14: 7–14.
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- RICHARDS, O.W. 1962. *A revisionary study of the masarid wasps (Hymenoptera: Vespoidea)*. British Museum (Natural History), London. 295 pp.



Masarina: *Celonites*

Celonites are $\pm$ 5–9 mm long—smaller than *Ceramius* ($\pm$ 10–20 mm long) but overlapping in size with *Jugurtia* ($\pm$ 7–15 mm long), *Masarina* ($\pm$ 5–9 mm long) and *Quartinia* ($\pm$ 2–7 mm long). The antennal club is rounded, like that of *Quartinia* but unlike that of the other genera of *Masarina* in which it tapers gradually towards the base. Like *Masarina*, they are stockily built but they are readily distinguished from *Masarina* and all the other genera except *Quartinia* by the relatively narrower head, the longitudinal folding of the wings at rest and in death, and by the ability to roll up in the same manner as cuckoo wasps (Chrysididae). At one time this ability led to the incorrect suggestion that they, like cuckoo wasps, might be labour parasites. The males are readily distinguished from the females by their smaller size and their strikingly larger antennal clubs (Figure 74).

Tongue length in *Celonites* is $\pm$ 3–6 mm, with the ratio of tongue length to body length $\pm$ 0.5–0.8.



FIGURE 74. Pair of *Celonites michaelsoni*, female on left (actual length $\pm$ 9 mm), male on right.

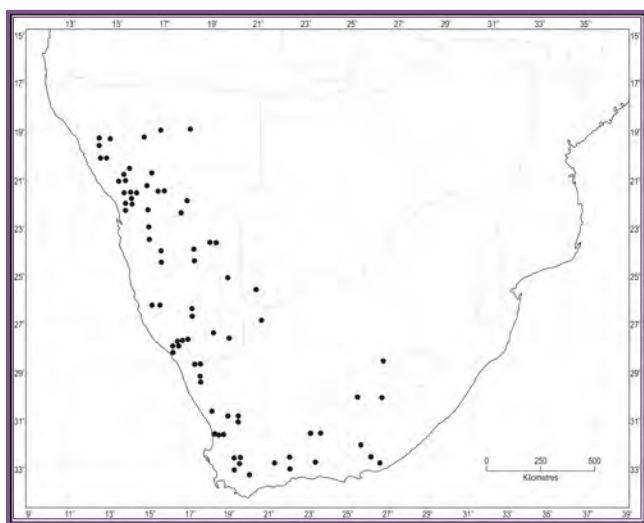


FIGURE 75. The known distribution of *Celonites* in southern Africa.

Distribution

There are 21 described species of *Celonites* in southern Africa. They are widely distributed throughout the Karoo Biome, are found in dry fynbos, on the dry savanna fringe and in drainage channels in the Namib Desert (Figure 75).

Flower visiting

Flower-visiting records are available for 15 of the southern African species of *Celonites* (Appendix 2). Together they have been recorded from flowers of 10 plant families, Scrophulariaceae, Campanulaceae, Asteraceae, Aizoaceae, Geraniaceae, Boraginaceae, Molluginaceae, Nyctaginaceae, Crassulaceae and Iridaceae.

All visits to Scrophulariaceae are for Aptosimeae, all three genera, *Aptosimum*, *Peliostomum* and *Anticharis*, being included. Seven species, 47%, *C. andrei*, *C. clypeatus*, *C. kalahariensis*, *C. michaelsoni*, *C. peliostomi*, *C. pulcher* and *C. tumidiscutellatus*, are specialist visitors of Aptosimeae, variously, in the Nama-Karoo from the southeast to the west and north through Namaqualand and Namibia to the Kunene River, in the southern Kalahari, in the Namib Desert and in the arid savanna of Namibia. Only two species, *C. andrei* and *C. michaelsoni*, have been recorded from any other flowers. On the eastern margin of the desert in northern Namibia two male *C. michaelsoni* were recorded from *Boerhavia deserticola* (Nyctaginaceae), not otherwise visited by any pollen wasps. In the eastern Nama-Karoo, when Aptosimeae were flowering sparsely, one female and one male *C. andrei* were recorded from *Lobelia anceps* (Campanulaceae). The only other records of visits by pollen wasps to *Lobelia* are from southeastern Namaqualand where a female and a male *Celonites lobeliae*, known from no other flowers, were recorded from *Lobelia linearis*.

Of the six species, 40%, of *Celonites* recorded from Campanulaceae, two, as noted above, were from Lobelioideae. The other four were from Campanuloideae, *Wahlenbergia* (including *Lightfootia*) and *Microcodon*. Of these, three species, namely *C. bergenwaliae*, *C. latitarsis* and *C. wahlenbergiae*, visit these flowers by preference.

Asteraceae have been recorded as receiving visits from five species, 30%. None of them except possibly *C. wheeleri*, are restricted to Asteraceae. *Celonites capensis*, recorded principally from Asteraceae from the southeastern Nama-Karoo, the Little Karoo and Namaqualand, has also been recorded in large numbers from *Pelargonium myrrhifolium* in the Little Karoo and variously in small numbers from *Prenia pallens* (Aizoaceae: Mesembryanthema), *Ehretia rigida* (Boraginaceae), *Wahlenbergia ecklonii* (Campanulaceae), *Phyllopodium cuneifolium* (Scrophulariaceae) and *Ferraria* (Iridaceae). For *C. promontorii*, recorded from Asteraceae in the Little Karoo, southern Nama-Karoo and southeastern Namaqualand, there are records of one female from *Pelargonium klinghardtense* in the Richtersveld and of two females from *Limeum* (Molluginaceae) in the southern Tankwa Karoo.

One species, *C. heliotropii*, is an abundant visitor in the company of *Jugurtia namibicola* to *Heliotropium tubulosum* (Boraginaceae) and, like it, appears to be a specialist. This is the only species recorded from Boraginaceae (apart from the record of one male *C. capensis* from *Ehretia*) in southern Africa.

However, this does not seem to be an uncommon preference in the Palaearctic where eight species of *Celonites* have been recorded from Boraginaceae, two from *Heliotropium*.

Aizoaceae, particularly the Mesembryanthema 'group', which are important forage plants for *Ceramius* groups 2A, 4, 5 and 8, appear to be secondary forage plants for only four *Celonites* species.

Two species of Palaearctic *Celonites* have been collected from Lamiaceae and a close association by *C. abbreviatus* (Villers) with this family has been suggested. This is of particular interest as in southern Africa *Celonites* have never been found to be associated with this family, not even as casual visitors.

(See figures under 'Pollen wasps as flower visitors and potential pollinators.')

Water visiting

There are no records of visits to water by any species of *Celonites*. It seems likely that all species use nectar as a bonding agent in the construction of nest cells.

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. michaelsoni* and putatively for *C. promontorii*. Earthen cells constructed in a pre-existing burrow in the ground are known for *C. wahlenbergiae*, *C. michaelsoni* and *C. arenarius*. Only one species, *C. latitarsis*, is known to excavate a burrow in which to construct its cells.

Description of nesting areas and 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 (Figure 5).

Celonites michaelsoni, widespread in karroid scrub and dry savanna, was found nesting only twice, in a rock crevice south



FIGURE 76. Nesting area of *Celonites latitarsis* in dry fynbos between Clanwilliam and Graafwater to the west of the Olifants River Valley; note molehill in the foreground.

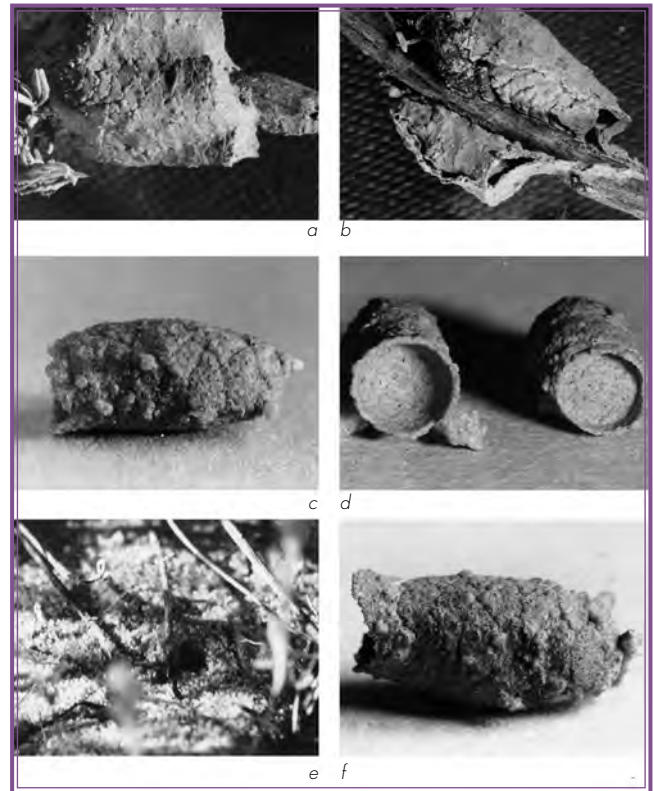


FIGURE 77a-f. a, b. putative nest of *Celonites promontorii* (actual length of nest 13 mm); c. cell of *C. wahlenbergiae*; d. two cells of *C. wahlenbergiae* showing incomplete cell with rounded blind end (left) and sealed completed cell (right) (actual diameter of seal 3.8 mm); e. nest entrance of *Celonites latitarsis*; f. cell of *C. latitarsis* (actual length 11 mm).

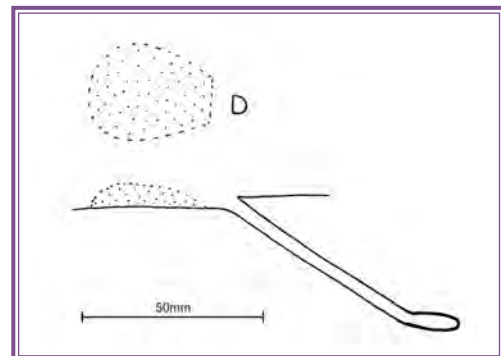


FIGURE 78. Nest of *Celonites latitarsis*: nest entrance and tumulus as seen from above (top); vertical plan (bottom).

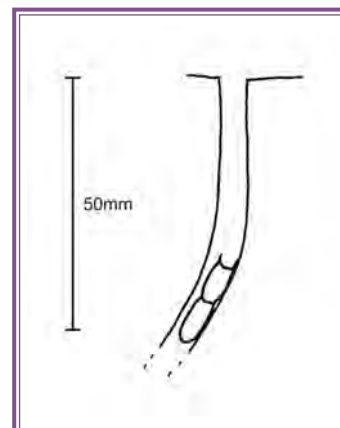


FIGURE 79. Vertical plan of nest of *Celonites wahlenbergiae*.

of the Orange River in the Richtersveld National Park and somewhat further east, north of the Orange, 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 (Figure 76). The soil in these areas is sandy, relatively coarse and loose on the surface but finer and more compact beneath. The finer sand is brought to the surface by the Cape Dune Molerat, *Bathyergus suillus* (Schreber) (Bathyergidae). The molehills stabilise, forming 'hillocks' of compacted sand in which the wasps nest, the former in a pre-existing burrow and the latter in a self-excavated burrow.

Description of nest

The only completely exposed aerial nest discovered by the authors was a putative nest of *C. promontorii*. It was on a stem of a dwarf shrub and consisted of a group of earthen cells arranged in contact longitudinally and with an earthen covering (Figure 77a, b). The other *Celonites* nests were all in protected situations. The cells of *C. wahlenbergiae* consisted of three linearly arranged earthen cells 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 (Figure 79). Both nests of *C. michaelsoni* 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 longitudinally attached.

The nest of *C. latitarsis* (Figure 78) consisted of an arched entrance (Figure 77e) leading to a short, sloping, self-excavated burrow terminating in a horizontal excavated cell. Within the excavated cell and of the same diameter was a constructed earthen cell (Figure 77f).

The cells of all species were ovoid, rounded at the closed end and somewhat truncate 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 (Figure 77c, f).

Method of construction of the nest

It seems likely that the method of cell construction is similar in all species. While 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 3 m and 2.5 m from the nests respectively. At the quarry site the wasp vibrated up and down vigorously while scraping up a load of sand, 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* and *Cotyledon dichotoma* respectively.

Each load of earth is added to the cell in the form of a semicircular 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 have been completed, 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. Sand excavated from the burrow is drawn out by the wasp as she reverses out of the 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, which differ from those of the other species of *Celonites*. The tarsi are more robust, are markedly expanded and are equipped with unusually stiff setae.

Re-use of nests

There is no evidence of the re-use of nesting cavities, nesting burrows or nest cells.

Provision

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 pollens was found to match only that from *Wahlenbergia paniculata* (Campanulaceae) and the other only that from a *Coelanthum* species (Molluginaceae) which was growing mixed with the *Wahlenbergia*. Although *Crassula dichotoma* (Crassulaceae) was visited by the nester, there was no pollen from this plant in the sample of provision examined. It is possible that it was being visited only for nectar. 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 were being used 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. michaelsoni* from the Richtersveld was pale grey, very moist but, having a papillate surface, barely touched the cell walls. Foraging records suggest that *C. michaelsoni*, *C. peliostomi*, *C. tumidiscutellatus* and *C. clypeatus* derive their provision from Aptosimeae (Scrophulariaceae).

Celonites heliotropii, which has been found solely foraging 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*, which is highly polyphagous, having been recorded from flowers of seven families, may well prove to be polylectic.

Sleeping and sheltering

The female *C. latitarsis* was observed to sleep within the nest at night and therefore, in inclement weather, would be expected to shelter within a nest that is being worked upon. It is likely that species nesting in cavities would behave similarly, as too would an aerial nester, if an open cell were available. *Celonites* have been observed by ourselves sleeping on grasses and narrow stems and in 1905 Brauns recorded a female *C. andrei* on a dry stem onto which it was holding with its mandibles.

Male behaviour

Males and females are present together at floral resources and males are occasionally observed perching on dry twigs or grasses in the vicinity of the forage plants. Early in the morning before the arrival of females, males are commonly present, resting on the ground, apparently waiting for the arrival of females, which they mount on the flowers. They are often rejected. Actual copulation has not been observed.

Associated organisms

Nest 'parasites'

Chrysididae, cuckoo wasps

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—*S. arnoldi* (Brauns) 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* species.

Currently recognised species

- C. andrei* Brauns, 1905; Northern Cape
- C. arenarius* Gess, 2007; Bushmanland, Northern Cape
- C. bergenwahliae* Gess, 1989; Western Cape and Namaqualand, Northern Cape
- C. capensis* Brauns, 1905; Western Cape and Eastern Cape
- C. clypeatus* Brauns, 1913; Eastern Cape and Northern Cape
- C. davidi* Gess, 1989; Richtersveld, Northern Cape

- C. humeralis* Richards, 1962; western Northern Cape
- C. heliotropii* Gess, 2007; northwestern Namibia
- C. kalahariensis* Gess, 2007; Northern Cape and Namibia
- C. latitarsis* Gess, 1992; Western Cape
- C. lobeliae* Gess, 1997; southwestern Northern Cape
- C. michaelsoni* von Schultze, 1923; Limpopo, Northern Cape and Namibia
- C. gariepensis* Gess, 1997
- C. peliostomi* Gess, 1989; Namaqualand, Northern Cape
- C. promontorii* Brauns, 1905; Western Cape, Eastern Cape and Free State
- C. pulcher* Gess, 2007; Namibia
- C. purcelli* Brauns, 1905; Eastern Cape
- C. tumidiscutellatus* Gess, 1997; Eastern Cape, Northern Cape and Namibia
- C. turneri* Richards, 1962; Northern Cape
- C. wahlenbergiae* Gess, 1989; Western Cape and Namaqualand, Northern Cape
- C. wheeleri* Brauns, 1905; Eastern Cape and Northern Cape

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requirements for successful nesting. *Transactions of the Royal Society of South Africa* 59: 23–27.

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GESS, S.K., GESS, F.W. & GESS, R.W. 1997. Update on the flower associations of southern African Masarinae with notes on the nesting of *Masarina strucki* Gess and *Celonites gariensis* Gess (Hymenoptera: Vespidae: Masarinae). *Journal of Hymenoptera Research* 6: 75–91.

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GESS, F.W. 1989. New species of the genus *Celonites* Latreille (Hymenoptera: Masaridae) from South Africa. *Annals of the Cape Provincial Museums (Natural History)* 18: 83–94.

GESS, F.W. 1992. A new species of the genus *Celonites* Latreille associated with the flowers of *Wahlenbergia* in southern Africa (Hymenoptera: Vespidae: Masarinae: Campanulaceae). *Journal of Hymenoptera Research* 1: 141–144.

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RICHARDS, O.W. 1962. *A revisionary study of the masarid wasps (Hymenoptera: Vespoidea)*. British Museum (Natural History), London. 295 pp.



Masarina: *Quartinia*

Quartinia (including *Quartinioides* and *Quartiniella*) are on average the smallest of the pollen wasps, ranging from $\pm 2\text{--}7$ mm in length. The largest species overlap in size with *Celonites* ($\pm 5\text{--}9$ mm long) and *Masarina* ($\pm 5\text{--}9$ mm long). Males tend to be slightly smaller than females but the difference is not as marked as in *Jugurtia* and *Celonites* (Figure 80).



FIGURE 80. Pair of *Quartinia femorata*, female on left (actual length ± 6 mm), male on right.

The larger species, those belonging to the genus *Quartinia sensu stricto*, have complete venation whereas with reduction in size through '*Quartinioides*' to '*Quartiniella*' there is a reduction in wing venation. Like *Celonites* but unlike all the other genera, their wings fold longitudinally and the antennal club is rounded. In the other pollen wasp genera the club tapers gradually towards the base. However, in general facies they are similar to all but *Celonites*, which are noticeably broad relative to their length.

In most species there is little readily discernable difference between males and females other than that the males are generally smaller than the females. However, in some species, for example *Q. bonaespei*, *Q. conchicola*, *Q. namaquensis*, *Q. vexillata*

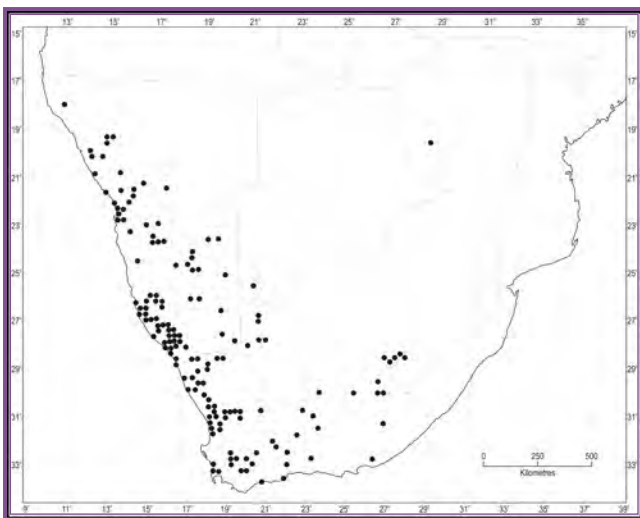


FIGURE 81. The known distribution of *Quartinia* in southern Africa.

and *Q. femorata*, the front legs of the males are greatly enlarged and modified. In some others, for example *Q. namaqua*, males bear a noticeable process on the underside of the gaster, like some species of *Ceramius*.

Like *Celonites*, they are able to roll themselves up. Some species readily roll out of flowers to avoid capture.

Tongue length in *Quartinia* is $\pm 2\text{--}5$ mm, with the ratio of tongue length to body length $\pm 0.4\text{--}1.1$. *Quartinia* is the only genus with species in which the tongue length is equal to or greater than body length. In the very long-tongued species, the tongue is looped several times when withdrawn into the glossal sac.

Distribution

There are 87 described species of *Quartinia* in southern Africa (75 listed below + 12 in the Addendum). A considerable number of additional species await description and naming. *Quartinia* is found throughout the distribution range of the Masarinae in southern Africa (Figure 81). Throughout the more arid areas, including the true desert, the Namib and southern extensions thereof, *Quartinia* is species diverse, 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 are currently being determined, but it is true to say that there are coastal species, coastal and inland desert fringe species that 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 (Appendix 2). Of the 40 species for which flower-visiting records are available, 75% have been recorded from Aizoaceae (including both Mesembryanthema and non-Mesembryanthema) and 58% from Asteraceae. Among these, 11 species, 27%, visit both Aizoaceae and Asteraceae, with a preference for one, both or neither. An appreciable number of species, 13%, 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. Among these species there are some with apparently definite preferences for flowers of one of these families. *Quartinia bonaespei* 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* from Campanulaceae than from Aizoaceae and Asteraceae, the other two families from which it has been recorded. *Quartinia poecila* 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*). In the southwest, *Limonium* appears to be an important secondary

forage plant for at least one species, which is, however, more commonly a mesemb-visiting species. In addition to Aizoaceae and Asteraceae, *Q. tarsata* also 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* from *Aloe striata* (Asphodelaceae) near Prince Albert in the southern Nama-Karoo.

Further flower-visiting records are available for 11 species (see Addendum). These fit into the overall picture of flower visiting by *Quartinia*. Of note is a species occurring in the Richtersveld, immediately south and north of the Orange River, that is frequently present in large numbers in the flowers of *Codon royerii* (Boraginaceae).

The importance of Asteraceae in southern Africa is reflected in North Africa, Iran and the Canary Islands where 10 of the 11 Palearctic species for which flower-visiting records are available have been recorded from Asteraceae, seven solely from Asteraceae.

(See figures under 'Pollen wasps as flower visitors and potential pollinators.')

Water visiting

There are no records of visits to water by any species of *Quartinia*. It seems likely that all species use self-generated silk as a bonding agent in nest construction.

Nesting

Nesting has been recorded for nine species of *Quartinia*, *Q. australis*, *Q. bonaespei*, *Q. conchicola*, *Q. namaqua*, *Q. namaquensis*, *Q. obibensis*, *Q. poecila*, *Q. refugicola* and *Q. vagepunctata*.

Description of nesting area and nest situation

Nesting by *Q. vagepunctata* in the Skuinshoogte Pass northeast of Nieuwoudville (Figure 40b) has been described. The nesting aggregation was in a bare patch, approximately 1 m², of



FIGURE 82. *Quartinia vagepunctata* nesting site; sand and silk nest entrance turret at left end of stone.

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 (Figure 82).

At least seven species of *Quartinia* nest in sand in the shells of terrestrial snails (Mollusca: Gasteropoda). Nests have been recorded from the sand-filled shells of several species of *Trigonephrus* (Dorcasiidae) (Figure 83) 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, but shells of an invasive exotic snail *Theba pisana* (Müller) (Helicidae) (Figure 84), 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 can house fewer cells and as the crown is low, the nest is less secure. Although historically *Trigonephrus* and *Tropidophora* (Figure 84) 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 *T. pisana* shells were 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 eastwards to Riet River in the Eastern Cape (Figure 85).



FIGURE 83. *Trigonephrus* sp. (Dorcasiidae).



FIGURE 84a, b. Shells (Mollusca, Gasteropoda) of *Theba pisana* (Helicidae), *Trigonephrus* (Dorcasiidae) and *Tropidophora ligata* (Pomatiidae) (actual width of shell of *Trigonephrus* 2.8 cm).

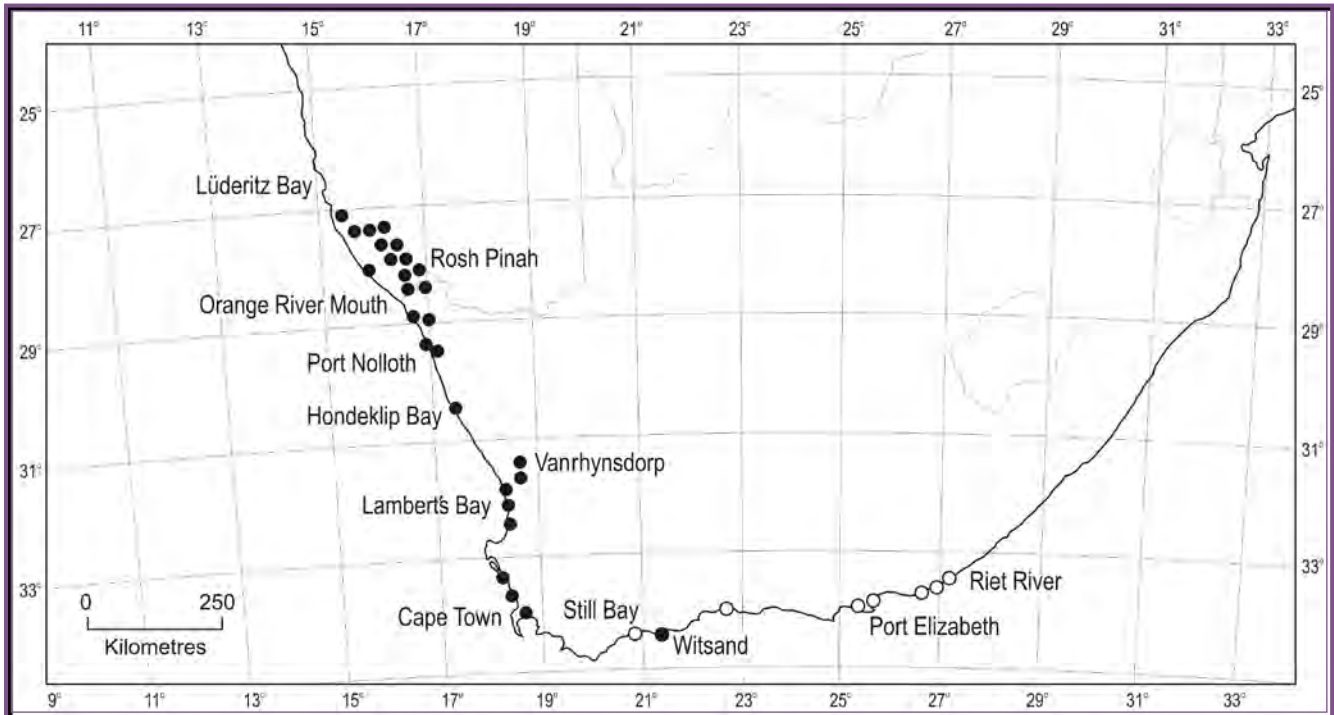


FIGURE 85. Distribution of snail shell sampling sites in southern Africa. Solid spots indicate sites at which *Quartinia* (Vespidae: Masarinae) was found nesting in snail shells.

Representation of species from snail shells:

- In the desertic winter-rainfall area north of the Orange River to south of Lüderitz Bay (Figure 86), *Q. obibensis* and *Q. refugicola* either singly or together.
- In the desertic winter-rainfall area south of the Orange River to Hondeklip Bay (Figure 87), *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 (Figure 88), *Q. conchicola*.
- In dune slacks along the coast from Donkinsbaai, north of Lambert's Bay, south to 4 km north of Blaauwbergstrand in the Blaauwberg Conservation Area north of Cape Town (Figure 89), *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.

Although in windswept sandy areas, where the ground is unstable, sand-filled snail shells represent the only microhabitat offering a secure nesting site for *Quartinia*, where rock outcrops occur, pockets of sand offer additional secure nesting sites. That such sites may be used by snail-shell nesters was confirmed by the discovery of *Q. refugicola* nesting in sand trapped in

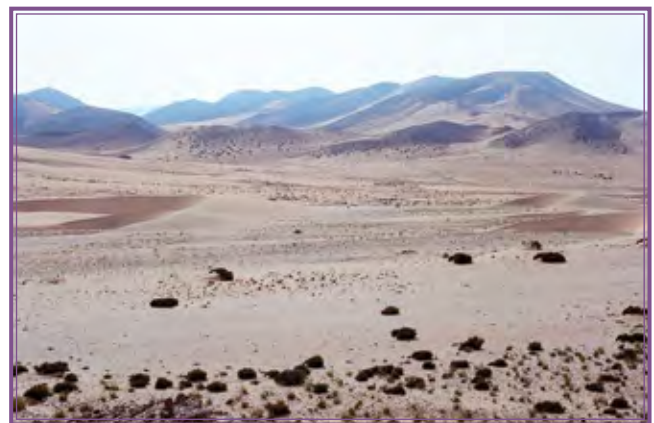


FIGURE 86. The Klinghardtberge, a sparsely vegetated desertic area in southwestern Namibia.



FIGURE 87. Shells of *Trigonephrus* southeast of Alexander Bay.



FIGURE 88. Southern Knersvlakte, sandveld patch, north of Vanrhynsdorp in the Western Cape.



FIGURE 89. Melkbosstrand, southwest coast, Western Cape, vegetated dune slack behind foredunes.



FIGURE 90. Sand-filled shell of *Trigonephrus*, showing entrance turret of *Quartinia*.

calcrete (Figure 91) in addition to sand trapped in snail shells. It is therefore clear that for *Q. refugicola*, at least, nesting in snail shells is not obligatory.

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*.

Description of the nest

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

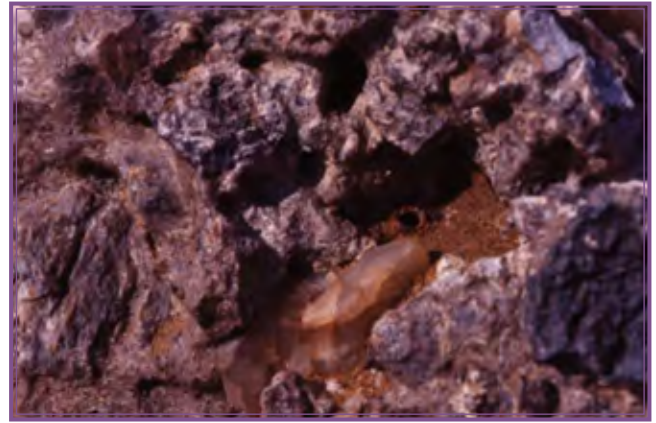


FIGURE 91. Sand-filled cavity in calcrete, showing nest entrance turret of *Quartinia*.

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: 0.16–1.20 mm in nests of *Q. vagepunctata*) held together by the silk.

The turret of *Quartinia* species nesting in snail shells is a simple short, erect cylinder of the same diameter as the burrow (Figure 90). 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, the opening to the burrow entrance at some short distance from the closed inner end of the bag (Figures 92, 93).

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 94). That of *Q. vagepunctata* consists of a subvertical shaft that terminates in a sealed, roughly ovoid cell. 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 only a short vertical shaft.

There appear to be no records of nesting by the Palaearctic species of *Quartinia*.

Method of construction of the nest

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 while constructing its nest. While joining together grains of sand with silk, it rotated its head, apparently issuing the silk from its mouth.

Provision

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). Pollen from the other three nests matched that of *Relhania* and *Cotula* (both Asteraceae).



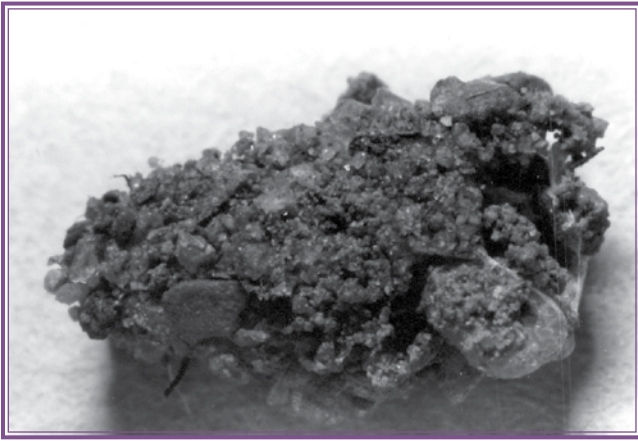


FIGURE 92. *Quartinia vagepunctata*, dorsal view of nest entrance turret.

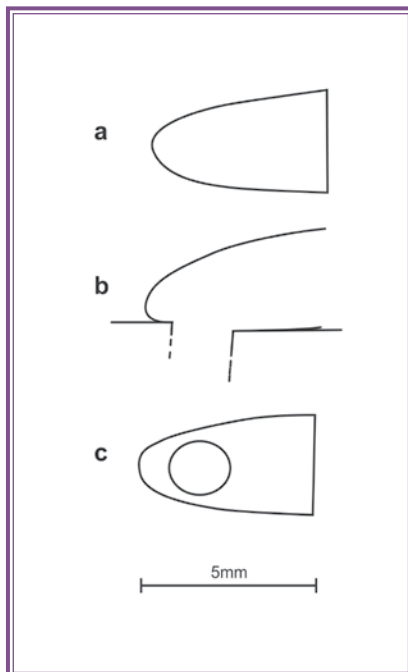


FIGURE 93. *Quartinia vagepunctata*, plans of turret: a. from above; b. vertical section; c. from below.

Sleeping and sheltering

When nests are being worked upon, sleeping or sheltering in the nest by females at night or in inclement weather is common amongst *Quartinia* species nesting in snail shells and would therefore be expected for species such as *Q. vagepunctata* nest-ing outside snail shells.

Male behaviour

Males and females are together at floral resources and males of *Q. vagepunctata* are present in the nesting area. Males wait for females in flowers or rest on the ground in the vicinity of forage plants and rise up in response to the arrival of females, which they then mount and copulate with on the flowers (Figure 95).

Associated organisms

Nest 'parasites'

Mutillidae, velvet ants



FIGURE 94. Two *Trigonephrus* shells broken open to show *Quartinia* cells within.



FIGURE 95a–c. *Quartinia* mating: a. a pair of *Q. femorata* mating on *Trianthema hereroensis*; b. a pair of *Quartinia* mating on a flower of *Drosanthemum*; c. a pair of *Quartinia* mating in a flower of *Codon royenii*.

Two species of mutillids, one of the genus *Tricholabiodes* (Figure 96) and one of an undescribed genus (both Sphaerophthalmi-nae: Dasyabrini), 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 pale orange and night-flying.

Chrysididae, cuckoo wasps

Allocoelia mocsaryi Brauns (Chrysidinae: Allocoeliini) has been reared from nests of *Quartinia* in snail shells (Figure 97) 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*.

Bombyliidae, bee flies

Apolysis hesseana Evenhuis & Greathead (Usiinae: Usiini) (Figure 98) 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. In nests from which *Apolysis* has emerged, the empty shuck is found attached to the outside of a *Quartinia* cell.



FIGURE 96a, b. *Tricholabiodes* sp. reared from nests of *Quartinia* nesting in *Trigonephrus* shells.



FIGURE 97. Cells and female of *Quartinia refugicola*, and associated *Allocoelia mocsaryi*, cocoon and imago (actual length of *Q. refugicola* $\pm$ 4.8 mm).



FIGURE 98. Cells and female of *Quartinia obibensis*, and associated *Apolysis hesseana* (actual length of *Q. obibensis* $\pm$ 5.4 mm).

Currently recognised species

- Q. alcestis* Richards, 1962; Western Cape
- Q. antennata* Richards, 1962; Western Cape
- Q. artemis* Richards, 1962; Northern Cape
- Q. atra* von Schulthess, 1929; Western Cape
- Q. australis* Gess, 2007; Western Cape
- Q. bonaespei* Gess, 2007; Western Cape
- Q. breyeri* Richards, 1962; ?
- Q. conchicola* Gess 2007; Western Cape and Northern Cape
- Q. femorata* Gess, 2007; Namibia
- Q. geigeriae* Gess, 2007; Northern Cape and Namibia
- Q. hypatica* Richards, 1962; Northern Cape
- Q. jocasta* Richards, 1962; Northern Cape and Namibia
- Q. lamellata* Gess, 2007; Namibia
- Q. media* von Schulthess, 1929; Western Cape
- Q. medusa* Richards, 1962; Namibia
- Q. namaqua* Gess, 2007; Western Cape and Northern Cape
- Q. namaquensis* Gess, 2007; Northern Cape
- Q. obibensis* Gess, 2007; Western Cape, Northern Cape and Namibia
- Q. ochraceopicta* von Schulthess, 1932, Namibia
- Q. paradoxa* Brauns, 1905; Eastern Cape
- Q. parcepunctata* Richards, 1962; Western Cape
- Q. perone* Richards, 1962; Western Cape
- Q. persephone* Richards, 1962; Western Cape and Northern Cape
- Q. pluto* Richards, 1962; Western Cape
- Q. prosperina* Richards, 1962; Northern Cape
- Q. punctulata* von Schulthess, 1930; Western Cape
- Q. refugicola* Gess, 2007; Northern Cape and Namibia
- Q. strucki* Gess, 2008; Northern Cape
- Q. vagepunctata* von Schulthess, 1929; Western Cape, Northern Cape and Namibia
- Q. vexillata* Gess, 2007; Northern Cape and Namibia



Species previously in *Quartiniella* von Schulthess, 1929

- Q. flava* (Richards), 1962; Northern Cape and Namibia
Q. minuscula (Turner), 1939; Eastern Cape
Q. striata (Richards), 1962; Northern Cape
Q. turneri (von Schulthess), 1932; Northern Cape and Namibia
Q. watersoni (von Schulthess), 1929; Western Cape and Northern Cape

Species previously in *Quartinioides* Richards, 1962

- Q. albopicta* (Richards), 1982; Namibia
Q. andromeda (Richards), 1962; Western Cape
Q. antigone (Richards), 1962; Western Cape
Q. arsinoe (Richards), 1962; Western Cape and Namibia
Q. basuto (Richards), 1962; Lesotho
Q. capensis Kohl, 1898; Western Cape and Eastern Cape
scutellimaculata von Schulthess, 1929 (in part)
Q. ceres (Richards), 1962; Western Cape, Eastern Cape and Northern Cape
Q. cressida (Richards), 1962; Western Cape, Northern Cape and Namibia
Q. cyllene (Richards), 1962; Western Cape and Northern Cape
Q. cynara (Richards), 1962; Western Cape and Eastern Cape
Q. diana (Richards), 1962; Northern Cape and Namibia
Q. dryope (Richards), 1962; Eastern Cape
Q. elissa (Richards), 1962; Western Cape
Q. eurydice (Richards), 1962; Northern Cape
Q. galataea (Richards), 1962; Western Cape
Q. hecuba (Richards), 1962; Western Cape, ? KwaZulu-Natal
Q. helena (Richards), 1962; Western Cape
Q. helichrysi (Richards), 1962; Lesotho
Q. hetaira (Richards), 1962; Western Cape
Q. interrupta Turner, 1939; Western Cape, Eastern Cape and Namibia
Q. iphigenia (Richards), 1962; Namibia
Q. laeta von Schulthess, 1935; Namaqualand, Northern Cape and Namibia
Q. latona (Richards), 1962; Western Cape
Q. maerens von Schulthess, 1935; Western Cape
Q. matabele Turner, 1939; Zimbabwe
Q. metallescens von Schulthess, 1929; eastern Northern Cape and Lesotho
Q. metope (Richards), 1962; Namibia
Q. minima von Schulthess, 1932; Namibia
Q. multiplicata (Richards), 1962; Western Cape
Q. niveopicta von Schulthess, 1930; Western Cape and Eastern Cape
Q. philomela (Richards), 1962; western Northern Cape

- Q. phoebe* (Richards), 1962; Western Cape
Q. poecila von Schulthess, 1930; Northern Cape and Namibia
Q. propinqua von Schulthess, 1932; Western Cape, Northern Cape and Namibia
Q. senecionis (Richards), 1962; Free State and Lesotho
Q. signata von Schulthess, 1929; Eastern Cape
Q. signatifrons Turner, 1932; Western Cape and Eastern Cape
Q. tarsata (Richards), 1962; Eastern Cape and Northern Cape
Q. titania (Richards), 1962; Western Cape

See Addendum: 12 new species of *Quartinia* described and published after the text had been finalised; 11 species with flower-visiting records.

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GESS, S.K. & GESS, F.W. 2004. The distributions of the genera of the pollen wasps (Hymenoptera: Vespidae: Masarinae) in the semi-arid to arid areas of southern Africa in relation to their requirements for successful nesting. *Transactions of the Royal Society of South Africa* 59: 23–27.

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Pollen wasps as flower visitors and potential pollinators

This section explores the flowers visited by pollen wasps in southern Africa and the potential of pollen wasps as pollinators of these flowers.

Flowers are the sole source of nourishment for both adult and larval pollen wasps. Like all the other wasps and the bees, both female and male adult pollen wasps require nectar for nourishment. Unlike all other wasp larvae feeding on invertebrate prey provided by the mother, pollen wasp larvae, like bee larvae, feed on pollen and nectar provided by the mother in the nest cells. For this reason, female pollen wasps, like bees, have to make more visits to flowers than other wasps.

Over the past 40 years we have been sampling flower visitation by aculeate wasps and bees throughout the semi-arid to arid areas of southern Africa. By 2003 the resultant database consisted of 16 229 records of visits by 972 species of wasps and bees to about 600 species of plants, representing 36 plant families. Of the plant families, 21 received visits from pollen wasps compared to 34 from non-*Apis* bees and 29 from nonmasarine wasps. Application of S.K. Gess's formula to establish comparative diversity of choice at the specific level showed a markedly narrower diversity of choice of flowers by pollen wasps than by nonmasarine wasps or bees. This indicated that pollen wasps as a group show a greater degree of oligophagy and narrow polyphagy than bees as a group. However, when the families of bees were taken individually, the bee families Colletidae and Melittidae were found to show a comparable degree of oligophagy and narrow polyphagy.

Although some pollen wasps do have relatively short tongues, most have long tongues, some considerably longer than the wasp's length from the frons to the tip of the abdomen (Figures 21, 22). Consequently, pollen wasps, like long-tongued bees (Apidae and Megachilidae), have the potential to obtain nectar from a wider range of flower forms than short-tongued wasps and short-tongued bees, most of which are obliged to visit flowers in which the nectar is readily accessible. This potential can either be used by any one species to visit a broad range of plant families or for the exploitation of specialist flowers with specialised structures that exclude short-tongued species from obtaining nectar. Whereas in the long-tongued bee families many species are broadly polyphagous, visiting up to 20 flower families, amongst the pollen wasps broad polyphagy is the exception, with only two species having been recorded from as many as seven flower families, most of which appear to be visited infrequently.

The 'pollen wasp pollination syndrome' falls within the syndrome designated as melittophily, but the flowers that pollen wasps visit are not necessarily equally efficiently serviced by bees and/or bee flies. Indeed, while pollen wasps visiting some flowers are members of a guild of flower visitors all of which are important potential pollinators, the pollen wasps visiting others are probably their most important potential pollinators. Furthermore, when considering the relative importance of pollen wasps as members of a guild, it is necessary to note whether all members of the guild are always present. Indeed, there are times and places

where the pollen wasps are the sole or most abundant potential pollinators present. In some instances this may relate to nesting requirements and in others to which other flowers are available at any one site. The latter is of importance where some members of the guild are polyphagous and others oligophagous. Under such conditions it is clear that oligophagous visitors will be more dependable than polyphagous species.

Requirements for a flower visitor to be a pollinator

All too often flower visitors are all loosely referred to as 'pollinators'. It is therefore necessary to have a clear understanding of the requirements for a visitor to be a potential 'pollinator'. For a flower to be pollinated by a visitor, that visitor must receive pollen from the flower in such a position that, when it enters a conspecific flower with a receptive stigma, some of that pollen is transferred to the stigma. For this to be successfully achieved, the visitor must in all but 'mess'-pollinated flowers follow a regular pattern of behaviour and 'fit' the flower.

It is essential that a pollinator should transport pollen, but the potential of an insect as a pollinator cannot be judged by its pollen requirements. Pollen that is deliberately collected by pollen wasps and bees and stowed away for transport by ingestion into the crop (pollen wasps and some colletid bees) or packed into external pollen carrying structures (most bees), is not available for pollination. Pollen that brings about pollination is free pollen that adheres, usually accidentally, to the carrier, not pollen purposefully collected for provisioning. Pollen that is free for pollination is just as likely to be collected and transferred by a visitor collecting nectar as by a visitor collecting pollen. Indeed, this transfer is most frequently performed by visitors seeking nectar rather than pollen. To achieve cross pollination, there must be movement between flowers. This is achieved if the nectar produced is enough to attract but not enough to satisfy.

If the visitor positions itself randomly, the chance of pollen being successfully transferred will also be random and the chances of its pollinating the flower will be random. If, however, the visitor positions itself regularly and this positioning is such that successful pollen transfer is brought about, then the chance of its pollinating the flower will be high.

Insect visitor size in relation to flower size is of variable importance. As with regularity of behaviour, good insect/flower fit generally increases in importance with an increase in flower complexity. Gullet flowers and campanulate flowers, for example, require a snug insect/flower fit. A relatively small insect is able to enter and leave these flowers, successfully obtaining nectar and pollen for its own use, without necessarily receiving a pollen load or coming into contact with the stigma. A relatively over-large insect on the other hand is not able to enter these flowers, but if it has a long enough proboscis, it may be able to rob a flower of nectar without receiving a pollen load or coming into contact with the stigma. For successful pollination of papilionate flowers, the size restraint is clearly not one of insect/flower fit in the sense of fitting snugly into the flower but of being of the correct size and weight to trip the mechanism that permits the release of the essential parts from the keel in which they are enclosed. A flower visitor that specialises in flowers of a particular taxon may successfully pollinate some and yet fail to pollinate others owing to size differences between flowers of different species, even of the same genus. Such species therefore

have a mutualistic relationship with some of the flowers that they visit and yet their visits to other flowers are only of benefit to themselves.

Care must be taken not to confuse monophagy and temporary fidelity. Having found a plant species in flower that proves to be a good resource, some insect visitors show temporary fidelity to flowers of that species. When the rewards diminish, such a visitor may transfer to flowers of an unrelated species to which it then shows temporary fidelity. While working flowers of a particular species, it may be servicing them more efficiently than a more dependable visitor. However, it may or may not be reliable on a year-to-year basis and is even less likely to be reliable on a locality-to-locality basis.

Pollinators show varying degrees of dependability and insect-pollinated flowers show varying degrees of specialisation with respect to 'acceptability' of insect visitors. One species of insect visiting only one species of flower (monophagy), the ultimate in dependability, is the exception. Oligophagous flower visitors are clearly more dependable than polyphagous species as the probability of their choosing a particular species of flower is greater. Where only one of their preferred flower species occurs in an area where other plants not favoured are in flower, they will clearly be expected and dependable visitors to that species. Such a plant may depend solely on the services of such an insect for pollination or may be serviced by a guild of oligophagous species that are either related or not related. In addition, they may even be randomly serviced by polyphagous species. Indeed generalist flowers that are pollinated randomly by a wide range of insects or at least a wide range of wasp and bee species may be amongst those plants favoured by oligophagous species. The evolutionary factors favouring specialist or generalist pollinators are not necessarily the same as those favouring specialist or generalist flowers.

Flowers visited by pollen wasps

The families of flowering plants in southern Africa attracting visits from pollen wasps are arranged below in order of the highest percentage of species visiting these taxa. The 2004 analysis was based on 129 species, including morpho-species, for which flower-visiting records were available. The present account is based on 107 species, all named species, some of which have been added since 2004.

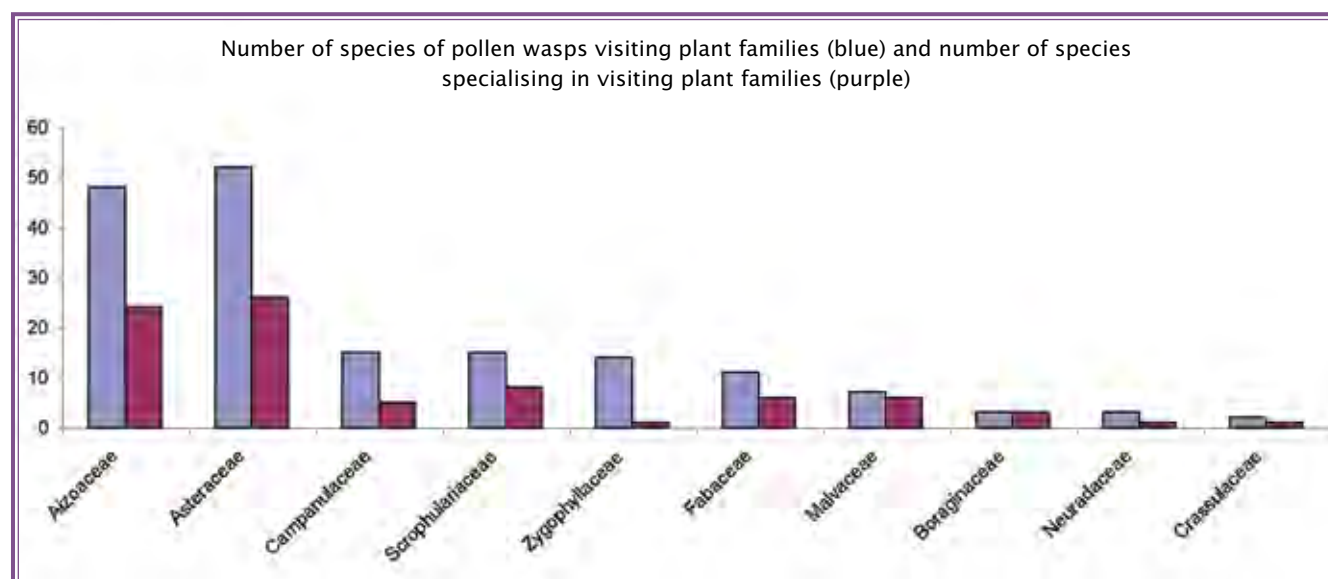
DICOTYLEDONS

Aizoaceae and Molluginaceae

The Aizoaceae and Molluginaceae have been variously delimited over time and the discussion continues. In the present work, Aizoaceae is seen to include the genera otherwise understood to form the family Mesembryanthemaceae, with the informal distinction Mesembryanthema and non-Mesembryanthema being used. Molluginaceae, previously included in Aizoaceae, is now seen as a separate family and as used here includes *Gisekia* and *Limeum*, which have at one time been included in the Phytolaccaceae and are currently being considered as representing two families, the Gisekiaceae and the Limeaceae.

Mesembryanthema shows its greatest diversity in western southern Africa but is represented by a few species around the Mediterranean Sea, in East Africa, the Arabian Peninsula, Madagascar, Australia, New Zealand and the adjacent islands. The non-Mesembryanthema are cosmopolitan in the tropics and subtropics of the southern hemisphere, with their centre of diversity in Africa. It is, however, only in southern Africa that pollen wasps have been recorded from the flowers of Aizoaceae.

Visits to Aizoaceae have been recorded for 48 named species of pollen wasps, that is 45% of the named pollen wasps for which flower-visiting records are available (Appendix 2). Specialisation has been established for 25 of these species. *Priscomasaris namibiensis*, nine species of *Ceramius*, two of *Jugurtia* and 13 of *Quartinia* are restricted to or show a marked preference for Aizoaceae. Clearly some of these species are dependent on the presence of Aizoaceae. Flowers of this family are visited throughout the Karoo Biome and associated fynbos, arid savanna, desert and coast. Distributions of species visiting Mesembryanthema (Figure 99) and non-Mesembryanthema (Figure 105) show marked differences. By far the largest number of species associated with Mesembryanthema was recorded from the winter-rainfall region, the area with the greatest diversity of Mesembryanthema and most extensive areas of 'mesemb veld' (examples in Figures 11, 100). North of the Orange River visits by pollen wasps to Mesembryanthema have been recorded only along the coast and short distances inland in drainage channels (examples Figures 17 and 18), reflecting the distribution of these



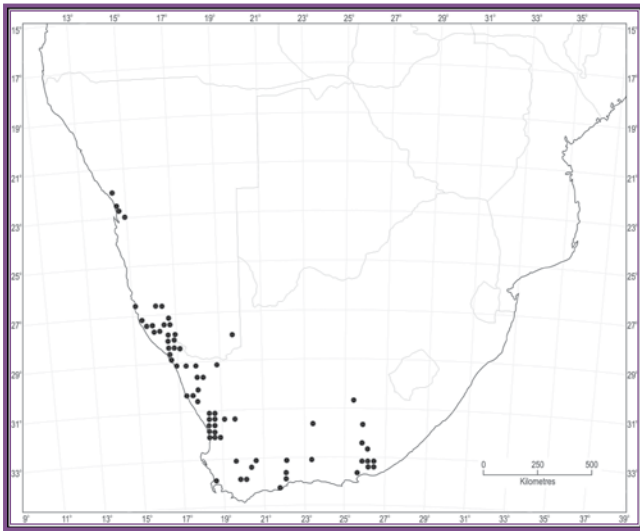


FIGURE 99. Known distribution of pollen wasps visiting Aizoaceae: Mesembryanthema.

plants. Indeed, there is a striking similarity between the overall distribution and nodes of species richness of mesembs and pollen wasps. South of the Orange River, 43% of pollen wasps visit mesembs and a high percentage of these are restricted to mesembs. They are considered to be efficient potential pollinators of the species they visit. During their flight period, which in the winter-rainfall areas is usually September and October, they are often the most abundant and dependable visitors, but in most cases are not the sole visitors or sole pollinators. Some earlier flowering mesembs are dependably visited by oligophagous fideiid bees (Megachilidae: Fideiinae), which are similarly considered to be efficient potential pollinators of the species they visit but again are not the sole visitors or sole pollinators. In the summer-rainfall areas and along the Namibian coast to the north, flight periods are more variable and pollen wasps and fideiid bees are commonly found in company, visiting mesembs.

The Mesembryanthema are most strikingly distinguished by the possession of petaloid staminodes. Whereas the flowers of non-Mesembryanthema and Molluginaceae are shallow, simple in form and mostly small to minute, those of Mesembryanthema are various in size and form—distinguished as stamen carpet flowers, central cone flowers, recess flowers and cup flowers (Figures 101–104). Most flowers have a distinct male and female phase, with the pollen being shed before the stigmas become receptive. When the pollen has been shed, the stamens wither and the receptive stigmas become prominent, elongate and present a receptive papillate surface.

The manner in which pollen wasps behave on mesemb flowers is largely dependent on both the flower form and the size of the flower in relation to the size of the wasp. Some examples will serve to clarify this point. Whereas large *Ceramius* species perch on the edge of small cone flowers and insert only the front of the head into the centre of the cone, very small species of *Quartinia* enter large cone flowers. Again large species of *Ceramius* 'perch' on the side of small carpet flowers whereas other pollen wasps that are small in relation to the size of the flower, walk around over the anthers (Figure 102b). Both receive pollen available for transport to receptive flowers and both are equally efficient potential pollinators.



FIGURE 100. Examples of 'mesemb veld': a. Knersvlakte, Namaqualand; b. Klipkoppe, Namaqualand; c. Richtersveld, Namaqualand; d. winter-rainfall desert edge near Aus, Namibia.

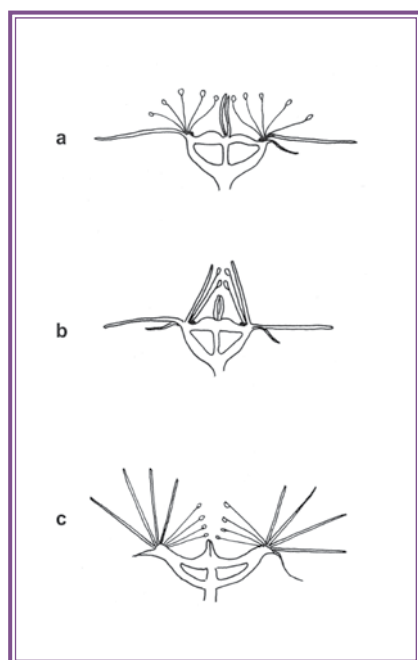
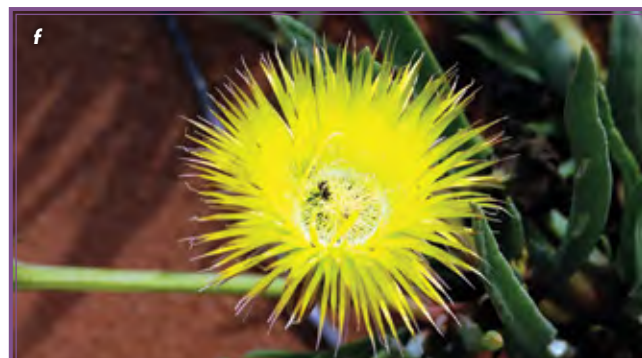
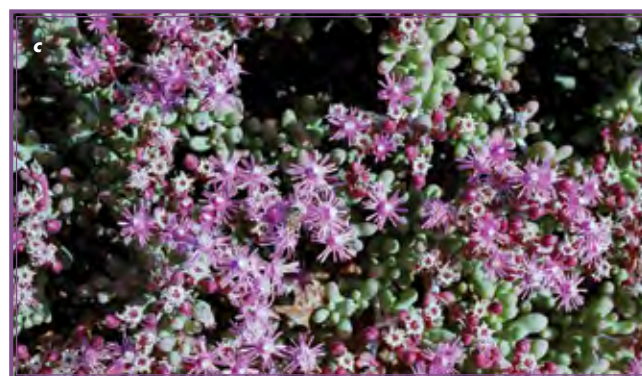


FIGURE 101a–c. Diagrammatic representation of three of the flower forms in Aizoaceae: Mesembryanthema: a. stamen carpet flower; b. central cone flower; c. cup flower.

No species of *Ceramius* have been recorded from the large-flowered mesembs of the genera *Conicosia*, *Carpobrotus* and *Herrea*. Those pollen wasps recorded as visitors are relatively small and are not likely to be the most efficient potential pollinators. *Conicosia* (Figure 102f), abundant in the Sandveld, is commonly visited by pollen wasps, most frequently of the genus *Quartinia* but also *Jugurtia* and *Celonites*. However, they are also visited by bees of several families, most notably Colletidae and Halictidae, which are larger, move around more in the flower and become coated with considerably more pollen. Clearly, these bees are more suited to pollinating such large flowers. The colletids, probably being oligophagous, are likely to be the most important pollinators.

In the west, *Carpobrotus* is visited by *Quartinia* but its most likely pollinators are large highly setose scoliid wasps, which are expected visitors and carriers of a considerable dusting of pollen.

Monkey beetles (Scarabaeidae: Hopliini) are common visitors to many mesemb flowers in the winter-rainfall areas. Many are



Above and right: FIGURE 102a–f. Examples of flowers of Aizoaceae: Mesembryanthema visited by pollen wasps: a. *Drosanthe-mum*, a stamen carpet flower; b. *Prenia tetragona*, a stamen carpet flower receiving a visit from *Quartinia*; c. *Ruschia*, a cone flower; d. *Stoeberia* receiving a visit from *Q. laeta*; e. *Herrea*, a cup flower; f. *Conicosia* receiving a visit from *Quartinia*.



FIGURE 103. A recess flower, *Dactyloopsis digitata*, receiving a visit from *Quartinia*.



FIGURE 104. *Ceramius peringueyi* in perching position on relatively small 'mesemb' flower, *Prenia pallens*.

destructive visitors but some, notably species of *Anisonyx*, are potential pollinators.

By comparison with Mesembryanthema, non-Mesembryanthema and Molluginaceae are relatively widely and abundantly visited by pollen wasps north of the Orange River, the percentage (42%) of species represented being equivalent to that (43%) of species visiting Mesembryanthema south of the Orange River where visits to non-Mesembryanthema and Molluginaceae are uncommon (Figures 105, 108). Pollen wasps near their nesting areas are often the most abundant visitors but in most cases are not the sole visitors or pollinators. The single species of *Ceramius*, *C. damarinus*, recorded from Namibia, specialises principally in visiting the showy purplish pink flowers of *Sesuvium sesuvioides* (non-Mesembryanthema) (Figure 106a) from southern Namibia, through western Namibia, to the Kunene River, together with a diversity of wasps and bees, amongst which in the south fidelid bees are at times equally abundant visitors. Minute-flowered *Trianthena hereroensis*, characteristic of the dune desert of the central Namib, was sampled in the northern extension of the dune desert between Walvis Bay and Swakopmund (Figures 106c, 107) where it was found to be

Right: FIGURE 106a–d. Examples of flowers of Aizoaceae: non-Mesembryanthema visited by pollen wasps: a. *Sesuvium sesuvioides*; b. *Trianthena parvifolia*; c. *T. hereroensis* being visited by *Quartinia femorata*; d. *Galenia africana*.



FIGURE 105. Known distribution of pollen wasps visiting Aizoaceae: non-Mesembryanthema.





FIGURE 107. *Trianthema hereroensis* as the dominant plant in the extension of the dune desert of the Namib to the north of Walvis Bay.

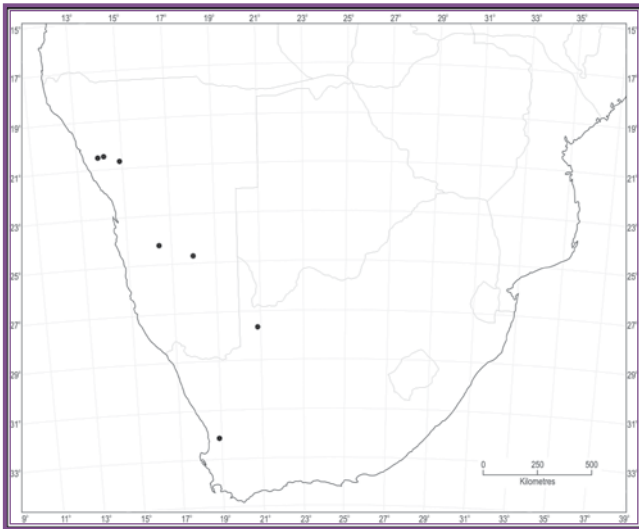


FIGURE 108. Known distribution of pollen wasps visiting Molluginaceae.

visited most commonly and abundantly by two sand-coloured species of *Quartinia*, *Q. albopicta* and *Q. femorata*. *Gisekia*, *Galenia* and *Limeum* with their small shallow flowers are visited by a wide range of wasps and bees, including pollen wasps. They are important to their pollen wasp visitors as forage plants and these pollen wasps are considered to be amongst their many potential pollinators. *Priscomasaris namibiensis* specialises in collecting nectar and pollen from non-Mesembryanthema, notably *Sesuvium sesuvioides* (Figure 106a) and *Trianthema parvifolia* (Figure 106b), and Molluginaceae, *Gisekia africana* (Figure 109d) and several species of *Limeum* (Figure 109a–c), all of which attract other pollen wasp visitors, most notably species of *Quartinia*.

Some species of both Mesembryanthema and non-Mesembryanthema are notably visited by fideliid bees and scoliid wasps, the former being specialist visitors.

Asteraceae

Asteraceae is the largest or second largest family throughout the Karoo-Namib. Generally Asteraceae are visited by a wide range of insect orders, notably Hymenoptera, Diptera, Lepidoptera, and Coleoptera. Though cosmopolitan and listed amongst the families visited by pollen wasps in the Palearctic and Nearctic, it is only in southern Africa that Asteraceae are visited by a high



FIGURE 109. Examples of flowers of Molluginaceae visited by pollen wasps: a. a prostrate species of *Limeum*; b. an erect species of *Limeum*, *L. sulcatum*, being visited by *Priscomasaris namibiensis*; c. *L. myosotis*; d. *Gisekia africana*.

percentage of species and throughout the region (Figure 110). All six tribes of Asteraceae characteristic of the semi-arid areas of southern Africa are visited by a wide range of families of wasps and bees. Visits to Asteraceae have been recorded for 52 named species of pollen wasps, that is 49% of the pollen wasps for which flower-visiting records are available (Appendix 2). Specialisation has been established for 26 of these species. Seven species of *Ceramius* and some species of *Jugurtia* and *Quartinia* are restricted to or show a marked preference for composites. Clearly some of these species are dependent on the presence of Asteraceae. The flowers of Asteraceae, composites, generally referred to as florets, are characteristically grouped in heads referred to as capitula. The capitulum is surrounded by few to many involucre bracts. In some groups, the heads are secondarily aggregated

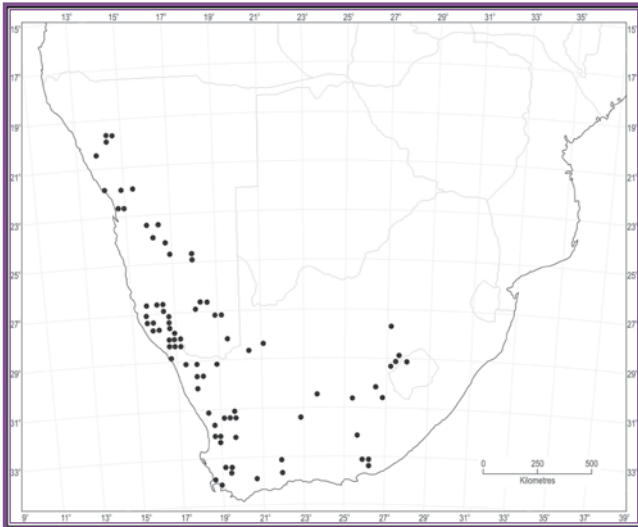


FIGURE 110. Known distribution of pollen wasps visiting Asteraceae.



Above & right: FIGURE 111. Examples of 'daisy' type Asteraceae visited by pollen wasps: a. *Arctotis laevis* being visited by *Ceramius braunsi*; b. *Tripteris microcarpa* being visited by *Quartinia*; c, d. *Leysera gnaphalodes* being visited by *C. nigripennis* (d showing pollen on the wasp); e. *Relhania pumila* being visited by *Q. vagepunctata*; f. *Geigeria pectidea* being visited by *Q. geigeriae*.



FIGURE 112. Further examples of Asteraceae visited by pollen wasps: a. *Berkheya schinzii* being visited by *Quartinia propinqua*; b, c. *Athanasia trifurcata* (b being visited by *Ceramius braunsi*, c being visited by *C. metanotalis*); d. *Pentzia sphaerocephala* being visited by *Q. vagepunctata*; e. *Pteronia pomonae*; f. *Felicia muricata*.

into cymose secondary heads. The florets are generally sessile on a common receptacle. The 'daisy' head combines a majority of fertile flowers, the disc florets, with an outer 'ring' of asexual ligulate florets, giving the capitulum as a whole a flower-like appearance (examples, Figures 111, 112).

The stamens are generally inserted on the corolla tube. The filaments are generally free and the anthers are united laterally to form a tube and are inwardly dehiscent. The ovary is inferior and the style slender, dividing at the top into two stigmatic lobes bearing hairs on the outer surfaces or at the tip. The style is generally surrounded at the base by a ring-like, shortly tubular nectary. As in the Campanulaceae (also Asterales), the stigmatic lobes are at first closely applied face to face and are surrounded by the anthers. After anthesis, the style elongates and the stigmatic head, which is hairy on its outer surface, carries the pollen aloft. Later the stigmatic lobes open, exposing their receptive surfaces. In some species, self-pollination is achieved in the absence of insect visitors by the stigmatic lobes curving backwards until the receptive surfaces come into contact with the pollen. To a great extent the power of self-pollination has been lost. Response by the anther tube to tactile stimulation is common. In response, the anthers contract and squeeze some pollen out at the upper end. Recovery is rapid and irritability is regained in less than half a minute. The florets open from the outer ones inwards so that the head is for some time purely male and for some time purely female, favouring cross-pollination.

Composites are widely visited by pollen wasps (Figure 110), the numbers and percentages of pollen wasp species being similar to those for Mesembryanthema in the south but being higher in the north where Asteraceae are widespread, unlike Mesembryanthema.

Species specialising in Asteraceae are distributed throughout the known range of pollen wasps visiting Asteraceae. Where pollen

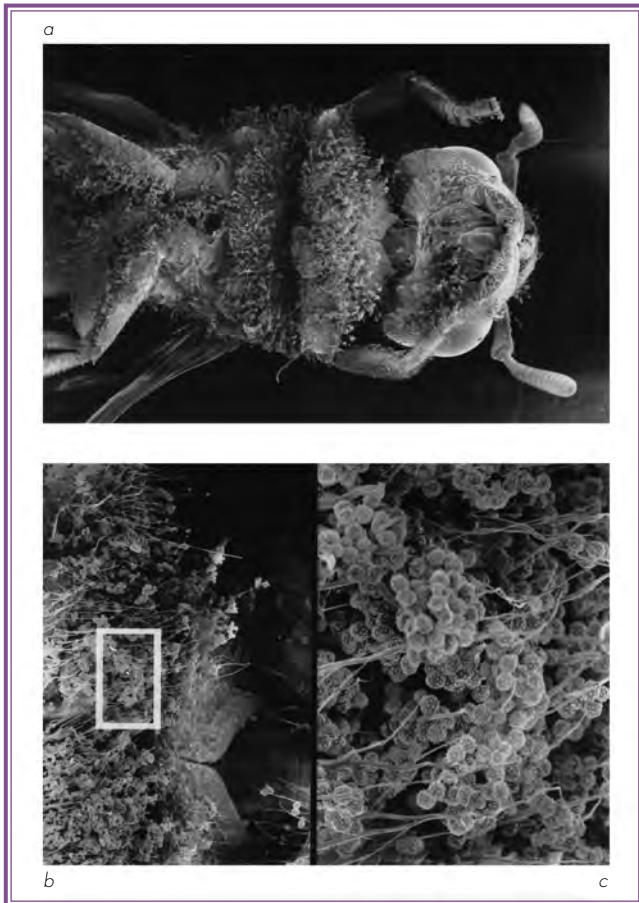


FIGURE 113. *Ceramius braunsi*: a. ventral view of anterior half of wasp showing pollen of *Arctotis laevis* (Asteraceae: Arctoteae) on hairy underside (actual width of head across eyes ± 3.6 mm); b. part of prosternum and base of front legs (actual width of boxed area ± 0.7 mm); c. boxed area enlarged.

wasps specialising in Asteraceae are common, they, particularly the specialists, are probably amongst the important pollinators of the species that they visit. In some areas they are probably indeed the most important pollinators.

The behaviour of a pollen wasp on a capitulum is governed by the size of the pollen wasp relative to the size of the capitulum. As a general rule, the diameter of the capitulum is such that the pollen wasp can alight on all six legs but if the pollen wasp is large in relation to the capitulum, it 'perches' on its rim. While imbibing nectar, it inserts its tongue into one floret after another, the insertion and removal resulting in a bobbing motion. When ingesting pollen, it rotates its short curved front legs in such a way that the pollen is brushed into its mouth. When engaged in both of these operations on a capitulum in the male phase, the pollen wasp is liberally coated with pollen on its undersurface (Figure 113) and when it visits another capitulum it will transfer pollen to stigmas presenting their receptive surfaces. The activities of the pollen wasp will furthermore be sufficient stimulus to trigger the 'irritable' behaviour of arctotid flowers. When a relatively large pollen wasp visits a relatively small capitulum and 'perches' on the rim, only the head, prosternum and the bases of the legs will receive a coating of pollen. Given the regular behaviour of pollen wasps, this would be sufficient for the transfer of pollen from one capitulum to another. Pollen wasps are thus potentially efficient pollinators. As a general rule, the composites visited by pollen wasps have a wider distribu-

tion than their pollen wasp visitors, but they may be visited by more than one species of pollen wasp throughout their range. For example, *Athanasia trifurcata* is visited by *Ceramius braunsi* (Figure 112b) to the south of Clanwilliam, by *C. metanotalis* (Figure 112c) to the north of Clanwilliam, and by *C. toriger* in the southern Tankwa Karoo south of Sutherland. In the vicinity of the nesting areas of these *Ceramius* species, the flowers are almost exclusively visited and pollinated by these pollen wasps, but in areas where *Athanasia trifurcata* is abundant but these pollen wasps are absent, the flowers are visited by diverse generalist visitors.

Scrophulariaceae

The cosmopolitan family Scrophulariaceae in southern Africa is visited by 16 named species of pollen wasps, that is 15% of the named pollen wasps for which flower-visiting records are available (Appendix 2), markedly fewer than visit Aizoaceae and Asteraceae. By contrast, in North America Scrophulariaceae are visited by seven species of *Pseudomasaris*, 31% of the pollen wasp species for which flower-visiting records are available for that region.

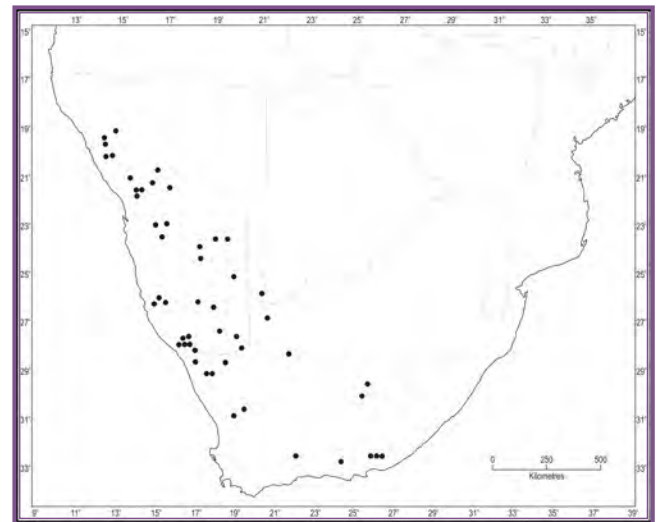


FIGURE 114. Known distribution of pollen wasps visiting Aptosimeae (Scrophulariaceae).

The Scrophulariaceae is one of the 10 largest plant families of the Karoo-Namib Region, but it is only with the Aptosimeae, *Aptosimum* (Figure 115), *Peliostomum* (Figure 117) and *Anticharis* (Figure 119), that there is a widespread association with pollen wasps (Figure 114). Specialisation has been established for eight species. Recorded visits by Masarinae to *Selago* (Figure 122) and *Phyllopodium* are secondary or casual and never represent specialisations.

The Aptosimeae are predominantly African, most species diverse in southern Africa and in particular in the dry west, with *Anticharis* extending into the Arabian Peninsula and India. In habit, Aptosimeae range from annual herbs to perennial prostrate 'mats' and shrublets. The flowers are various shades of bluish violet to purplish violet. They are 'gullet flowers', with the corolla 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 (Figures 116, 118, 120). The greater part of the corolla tube is wide but the lower surface is invaginated, requiring all but the smallest visitors to push their way into the



FIGURE 115. Examples of *Aptosimum* flowers: a, b. *A. spinescens*; c. *A. arenarium*; d. *A. procumbens*.

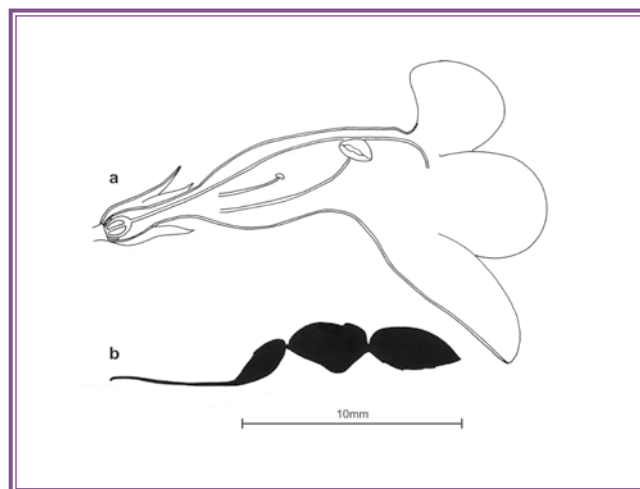


FIGURE 116. *Aptosimum procumbens*: a. diagrammatic longitudinal section of flower; b. profile of *Celonites clypeatus* (legs and wings omitted) to demonstrate wasp/flower fit.



FIGURE 117. *Peliostomum* flowers: a. *Celonites peliostomi* approaching flower; b. *C. peliostomi* entering flower; c. *Masarina peliostomi* entering flower.

flower. There are four stamens in two pairs, a pair with relatively long filaments and the other pair with relatively short filaments. In *Aptosimum* the shorter pair of stamens are 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 at the mouth of the corolla, but with time the style elongates and curves downwards.

In the course of our study of wasps and bees in the semi-arid areas of southern Africa we have observed the visitors of many species of these plants throughout the eastern, southern, western and northern Karoo as far north as the Kunene River, in the southern Kalahari and in drainage channels through the Namib Desert. Everywhere they were visited principally by pollen wasps and in some areas, particularly in the north, to a lesser extent by bees. Throughout, their principal visitors are species of *Celonites*, *C. andrei*, *C. clypeatus*, *C. kalahariensis*, *C. michaelsoni*, *C. peliostomi* (Figure 117a, b), *C. pulcher* and *C. tumidiscutellatus*, in some areas together with several species of *Quartinia* and, only in the northern Richtersveld, with *Masarina peliostomi* (Figure 117c), which is known only from this area.

Specialist *Celonites* species are considered to be the most important pollinators of these plants. They are ideal pollinators as they fit snugly into the flowers and, when drinking nectar, are obliged to penetrate deeply into the flower as the extended tongue matches the length of the narrow tube at the base of which the nectaries are situated (Figures 116 and 118). In this position the hind end of the wasp's thorax is immediately beneath the

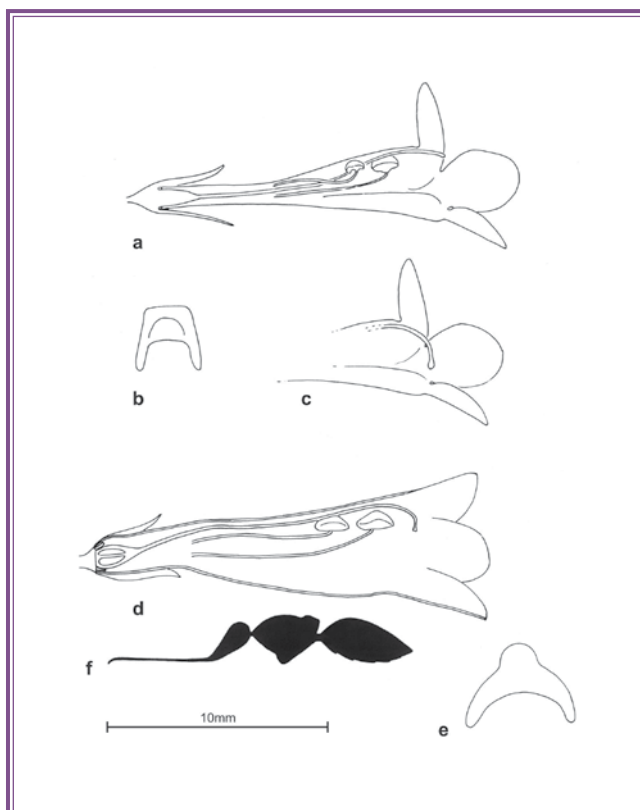


FIGURE 118. *Peliostomum leucorrhizum* flower: a. diagrammatic longitudinal section before style elongation; b. cross section to show invagination; c. partial longitudinal section after style elongation. Middle, *P. virgatum* flower: d. longitudinal section; e. cross section to show ventral invagination. Bottom, f. profile of *Celonites peliostomi* (legs and wings omitted) to demonstrate wasp/flower fit.



FIGURE 119. Examples of *Anticharis* flowers: a, b. *A. scoparia*, southwestern Namibia; c, d. *A. inflata*, northwestern Namibia.

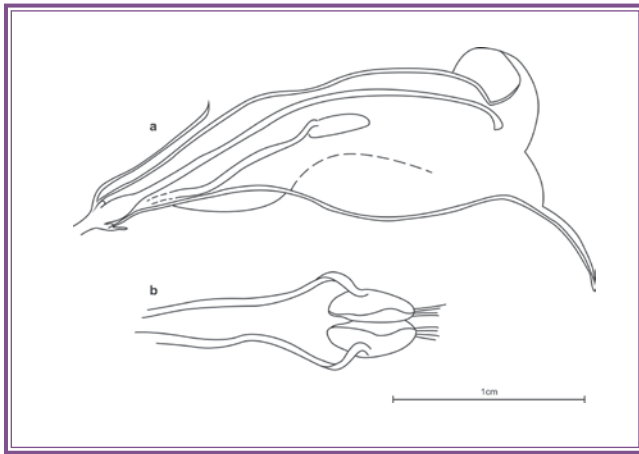


FIGURE 120. *Anticharis scoparia*: a. diagrammatic longitudinal section of flower; b. diagrammatic view of stamens from above.

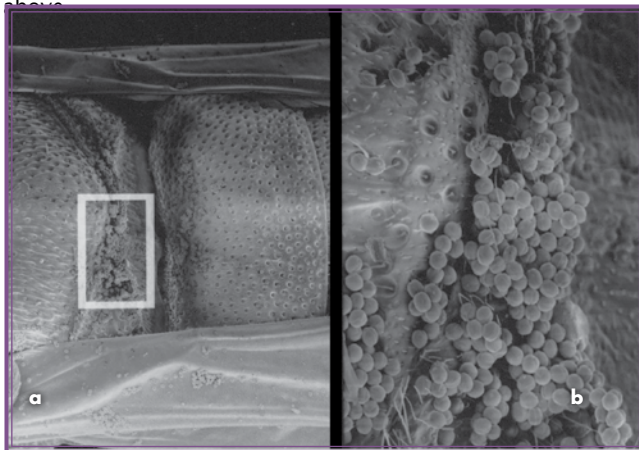


FIGURE 121. *Celonites peliostomi*: a. dorsal view of posterior end of thorax and anterior end of abdomen, showing deposition of pollen (actual width of boxed area ± 0.7 mm); b. boxed area enlarged.

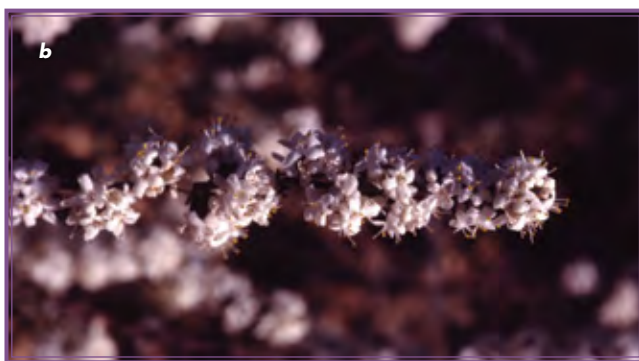
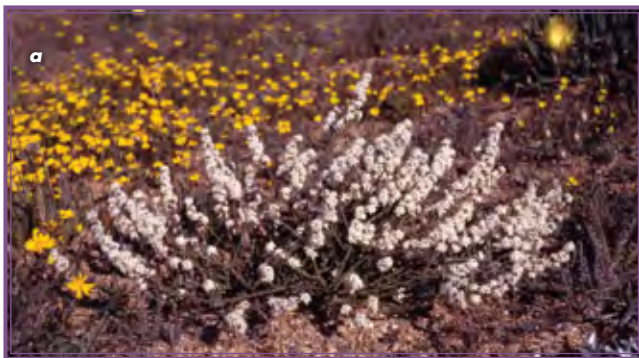


FIGURE 122a, b. *Selago* sp. visited by *Jugurtia braunsi* in the Kamiesberg, Namaqualand.

anthers which, when ripe, deposit a load of pollen onto the back of the wasp (Figure 121). In fact, it seems likely that in common with some other gullet flowers, the dehiscence of the anthers is probably triggered by the insect visitor. A wasp emerging from a flower after having been liberally showered with pollen, visibly bears a blue-grey dusting. Such a wasp, when entering a flower in which the stigma has elongated so that the receptive stigma is pointing downwards, inevitably wipes off some of the pollen and, in so doing, pollinates the flower.

The *Quartinia* visitors, with one possible exception, are not specialist visitors and are generally too small to be pollinators, except where flowers are undersized. The highest number of masarine genera and species visiting Aptosimeae has been recorded from the northern Richtersveld where, in addition to species of *Celonites* and *Quartinia*, *Masarina peliostomi* and *Jugurtia codoni* are among the visitors and the former, at least, is considered to be a specialist and additional potential pollinator. Indeed in this area the percentage of species visiting Aptosimeae is exceptionally high, on a par with Aizoaceae and Asteraceae, including not only an exceptional number of specialist pollen wasp visitors but also an almost equal number of casual visitors with other specialisations.

Visits from bees are very uncommon in the south but in Namibia and the Kalahari north of the Orange River, visits from bees are sufficiently frequent to be expected. Sixteen species of bees were recorded, most being infrequent casual visitors. Some were, however, encountered at several sites: *Meliturgula haematospila* Cockerell (Andrenidae: Pangurinae); and *Nomia* (*Acnomia*) *epileuca* Cockerell and *Pseudapis cinerea* (Friese) (both Halictidae: Nomiinae). Unlike the pollen wasps, all of which have long tongues, none of the bees are equipped to reach the nectar at the base of the corolla tube. *Meliturgula haematospila* is a small, flattened bee, which would not activate the release of pollen. It is possible that the nomiines, in forcing themselves into the flower, might do so. All the bees are polyphagous, *M. haematospila* having been recorded from nine plant families and the two nomiines from 14 and 12 families, respectively.

Campanulaceae

Campanulaceae are cosmopolitan but most diverse in the Mediterranean region and southern Africa. There are three subfamilies, the Campanuloideae, with regular flowers and free

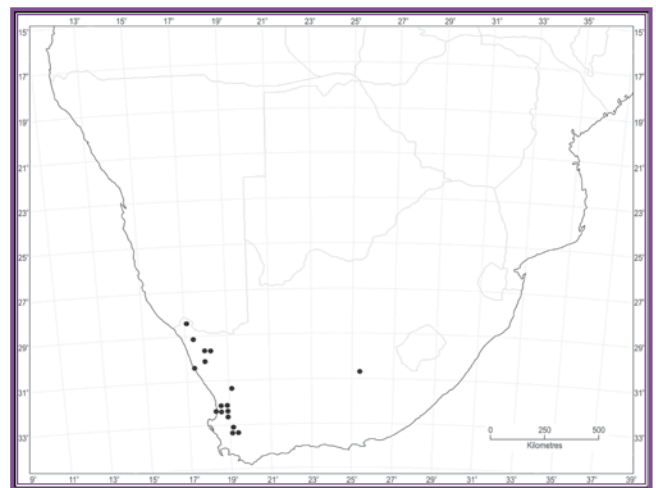


FIGURE 123. Known distribution of pollen wasps visiting Campanulaceae.

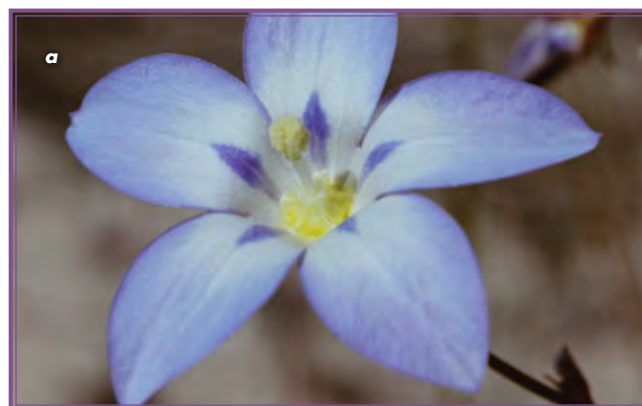


FIGURE 124. Examples of deeply campanulate *Wahlenbergia* flowers: a. *W. psammophila*; b, c. *W. pilosa*; d. *W. prostrata* being visited by *Quartinia*.

Right: FIGURE 125. Examples of shallowly campanulate, stellate *Wahlenbergia* flowers: a, b. *W. annularis*; c. *W. annularis* being visited by a melittid bee, *Capicola nigerrima*; d. *W. namaquana*; e. *W. capensis* being visited by a monkey beetle, *Peritrichia pseudursa*.



anthers, the Lobelioideae, with highly irregular resupinate flowers and connate anthers, and the Cyphioideae, a small group of transitional genera, all represented in southern Africa. It is only in southern Africa that visits by pollen wasps have been recorded. Records are available for 15 named species of pollen wasps, that is 14% of the named pollen wasps for which flower-visiting records are available (Appendix 2). Specialisation has been established for five species.

In the Campanuloideae, the genera *Wahlenbergia* (including *Lightfootia*), most species diverse in the southwest, and *Microcodon*, endemic to the southwest, are visited abundantly by pollen wasps in the southwest (Figure 123) where the number and percentage of species visiting them, though far less than visiting Mesembryanthema and Asteraceae, is next highest, as are the numbers and percentages of species specialising in them. Although *Wahlenbergia* has been sampled in the north and southeast, no pollen wasps have been recorded visiting them in these areas.

Wahlenbergia plants are mostly annual or perennial herbs, most of which are erect although some are straggling. Some are woody dwarf shrubs. The number of calyx lobes, corolla lobes, and stamens is almost invariably five. In many species, the corolla is campanulate, with a distinct corolla tube and more or less broad lobes (Figure 124). From this generally primitive state, there is a tendency toward a shortening of the tube and a narrowing of the lobes, giving the corolla a stellate appearance (Figure 125). The stamens alternate with the petals. In some spe-

cies the filament bases are expanded. The anthers are either free or attached to the corolla. The position of the ovary varies from inferior to subsuperior. The lower part of the style is smooth or hairy, and the upper part is variously clad with pollen-supporting hairs (Figure 126).

In the bud, the ripe anthers form a tube through which the style grows, pushing the stiff pollen-collecting hairs through the thecae and clearing them of pollen. In the newly opened flower the pollen coats the upper part of the style and the outer surfaces of the closed stigmatic lobes, giving the whole a club-like appearance. After the flower has been open a little while, the hairs supporting the pollen disappear, apparently by invagination, and the pollen falls, being retained within the corolla in deep-flowered species but falling free in species with a shallow stellate corolla and a long style. The style lobes then separate and present their receptive surfaces. The nectar-secreting tissue on the upper surface of the ovary of all the species with deep campanulate flowers is uncovered, except in some species by hairs projecting from the style. That of the species with shallow stellate flowers is covered by the bases of the filaments, which are expanded and closely adpressed to it. Nectar is produced on the top of the ovary.

Exceptional in flower form is *Wahlenbergia capensis* (L.) A. DC. (Figure 125e), a species found in the southwest. The corolla is stellate and the nectar is protected by the expanded bases of the filaments, but the style is shorter and when the flower opens the stigmatic lobes are already separating so that the pollen is not presented on a 'club' but on the underside of the expanded stigmas. Another striking and unusual feature is that the centre of the flower bears dense, brown hairs.

The free lobes of the corolla of the open flowers of all species show 'sleeping' movements. The flowers open at midmorning, close at mid- to late afternoon, and reopen at midmorning the following day. Some wasps, including pollen wasps, and bees make use of this phenomenon for night-sheltering.

Pollen wasps have been shown to collect both nectar and pollen from narrow-tubed flowers of *Wahlenbergia* and *Microcodon* and to be their most important potential pollinators in the west, south of the Orange River. When visiting these flowers, a pollen wasp alights on the outwardly curved corolla lobes before entering (Figure 124d), so that when it enters a newly opened flower to drink nectar, its dorsal surface brushes against the pollen-clad style and becomes coated with pollen. When a pollen wasp comes from such a newly opened flower and then enters a flower in which the stigmatic lobes have spread out, pollen will be transferred from it to the receptive stigma.

Pollen wasps less commonly visit stellate flowers to harvest pollen from the pollen-laden 'club' but have not been seen drinking nectar, which is closed to them as they alight on the corolla lobes when entering flowers. In behaviour they are therefore not suited to be pollinators of these flowers. The nectar is, however, available to specialist melittid bees, which are the pollinators of these flowers, notably several species of *Capicola*, relatively large *C. danforthi* Eardley and *C. nigerrima* Cockerell (Figure 125c) associated with *Wahlenbergia annularis* and relatively small *C. rhodostoma* Cockerell associated with the small flowers of *W. namaquana*. A melittid bee reaches the nectar by inserting its mouthparts at the open ends of the expanded filament bases. This it achieves by entering the flower with its ventral surface towards the style. Thus, when entering a newly opened flower

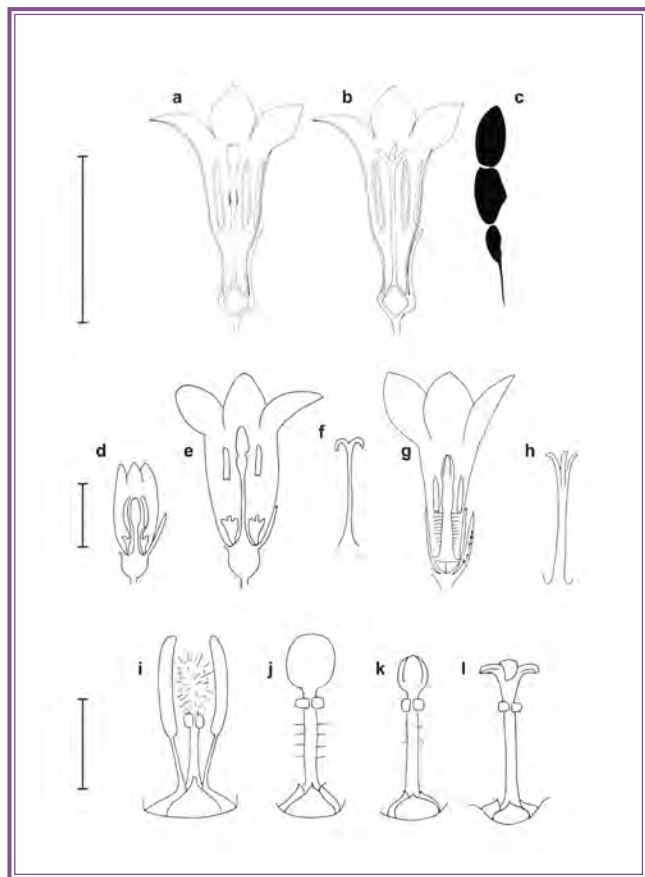


FIGURE 126. *Wahlenbergia*, diagrammatic longitudinal sections of flowers: a, b. *W. paniculata* with profile of c. *Quartinia parcepunctata*; d-f. *W. psammophila*; g, h. *W. pilosa*; i-l. *W. annularis* (scale bar = 5 mm).



FIGURE 127. Lobelioideae: *Lobelia* flowers visited by pollen wasps, a. *L. linearis*, southeastern Namaqualand, and b. *L. anceps*, eastern Nama-Karoo; c. *Monopsis debilis* visited solely by *Haplomelitta ogilviei*.

to drink nectar, its ventral surface brushes against the pollen-clad style and becomes coated with pollen. When a melittid bee comes from such a newly opened flower and then visits a flower in which the stigmatic lobes have spread out, pollen will be transferred to the receptive stigma.

Wahlenbergia capensis is visited neither by pollen wasps nor melittid bees, but by 'hairy' monkey beetles *Peritrichia pseudursa* (Scarabaeidae: Hopliini), which are its pollinators (Figure 125e).

Pollen wasps have not been recorded from *Wahlenbergia* north of the Orange River or in the southeast where these flowers appear to be serviced by nonspecialist bees.

Few flower-visiting records have been obtained for Lobelioideae, with the exception of *Monopsis debilis*, which is common in damp places in the southwest at localities where *Wahlenbergia*, abundantly visited by pollen wasps, is also present. It is always visited solely by a melittid bee, *Haplomelitta ogilviei* (Cockerell)

(Figure 127c), which is considered to be its pollinator, never even casually by pollen wasps.

Visits to *Lobelia* by small carpenter bees, Ceratinini (Apidae: Xylocopinae), have been recorded in both the southwest and southeast. At only two sites, one near Nieuwoudtville in the southwest and the other near Colesberg in the southeast, were pollen wasps found to be visitors. At the Nieuwoudtville site, visitors to *L. linearis* (Figure 127a) were observed over several days. The flowers received visits from *Celonites lobeliae* and *Ceratina*, a nonspecialist bee. Both, in size and fit, are potential pollinators but, as *C. lobeliae* has not been recorded from any other flowers, it may well be more dependable.

At the site near Colesberg *Lobelia anceps* (Figure 127b) was observed over several days. It was visited by *Celonites andrei*, 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.

Zygophyllaceae

Zygophyllaceae are most abundant in the tropics and subtropics, mainly in hot, arid, alkaline regions. They are herbs, shrubs, undershrubs, rarely trees. The leaves are often fleshy. The flowers are bisexual, rarely unisexual, regular or irregular and are borne singly or on a cymose inflorescence. Visits to Zygophyllaceae by pollen wasps have been recorded only in southern Africa. Fourteen named species of pollen wasps, that is 13% of the named pollen wasps for which flower-visiting records are available, were collected from flowers of this family (Appendix 2). Specialisation has been established, but for one species only.

In southern Africa, the greatest species diversity and the greatest abundance of individuals is encountered in the west. Wherever the genera *Zygophyllum*, *Tribulus* and *Sisymbrium* occur, they are visited variously by several families of bees and the two former by wasps. Visitation of *Zygophyllum* by bees was recorded from the Olifants River Valley northwards but visitation in addition by wasps, including pollen wasps, was recorded only from the Richtersveld northwards (Figure 128). In the Richtersveld we recorded five species of pollen wasps of the genera *Ceramius*, *Jugurtia* and *Masarina* and in western Namibia six named

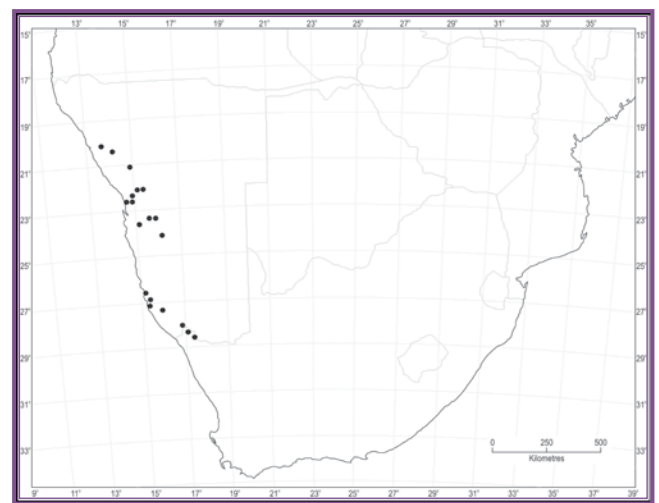


FIGURE 128. Known distribution of pollen wasps visiting Zygophyllaceae.



species of pollen wasps, *Priscomasaris namibiensis* and five species of *Quartinia*. All are potential pollinators, but the only pollen wasp visitors, which are possibly specialists, are four species of *Quartinia* in the northwest where they are expected visitors to *Zygophyllum simplex*. (Examples of *Zygophyllum* species visited by pollen wasps, Figure 129)

Fabaceae

The cosmopolitan family Fabaceae is one of the 10 largest plant families occurring throughout the Karoo-Namib region. The three subfamilies, Papilionoideae, with 'pea' flowers, Mimosoideae, with small flowers crowded into heads crowned by the numerous stamens, and Caesalpinioideae, with medially zygomorphic flowers generally with free, relatively large petals and anthers apically poricidal, show very different patterns of flower visitation. Visits to Fabaceae have been recorded for 11 named species of pollen wasps, that is 10% of the named species for which flower-visiting records are available (Appendix 2). Specialisation has been established for six species.

Apart from some bird-pollinated taxa, the Papilionoideae are principally visited and pollinated by guilds of bees, the representation by taxa varying between the flower taxa and relating to flower size and structure. However, *Aspalathus* (Figure 131), *Lebeckia* (Figure 132) and *Wiborgia* (Figure 133) (all Cape Crotalariaeae (*sensu* Polhill)) also attract visits from pollen wasps. Pollen wasps were represented in samples from *Aspalathus*, *Lebeckia* and *Wiborgia* in Namaqualand and from there southwards to the Cape (Figure 130). Three species of *Ceramius*, *C. clypeatus*, *C. richardsi* and *C. micheneri*, are apparently restricted to *Aspalathus* and two species of *Masarina*, *M. familiaris* and *M. hyalinipennis*, are apparently restricted to *Aspalathus*, *Lebeckia* and *Wiborgia*.

FIGURE 129. Examples of *Zygophyllum*: a, b. *Z. prismatocarpum*; c, d. *Z. simplex*; e, f. *Z. stapfii*.

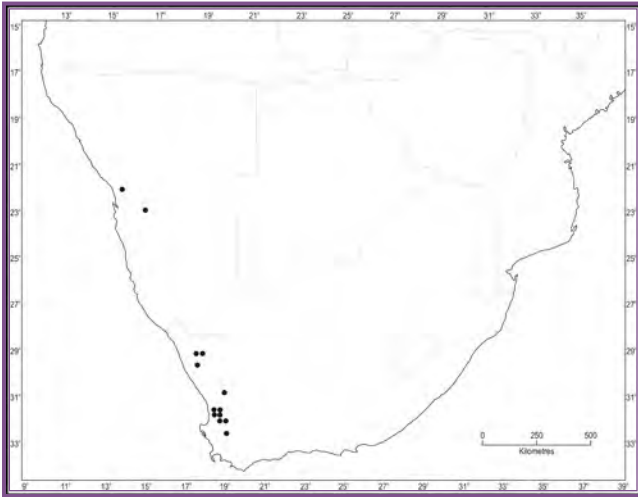


FIGURE 130. Known distribution of pollen wasps visiting Fabaceae, Caesalpinioideae to the north and Papilionoideae to the south.

All three species of *Ceramius* trip the flowers when they alight on the wing petals and reach into the flower to obtain nectar (Figures 134b, 135a). The keel opens and the insect receives a dollop of pollen far forward on its underside (Figure 136). As these insects always alight in the same way, they will carry this pollen to other flowers, which will be pollinated if the stigma is receptive. The smaller pollen wasps, the two species of *Masarina*, have a different technique for entering the flowers. They trip the flowers when they alight on the standard and reach into the flower to obtain nectar (Figures 134c, 135b). The keel opens and the *Masarina* receives a dollop of pollen on the front of its head (Figure 137). Again, as these pollen wasps always alight in the same way, they will carry this pollen to other flowers, which will be pollinated if the stigma is receptive. Within their distribution ranges, these pollen wasps will be the most dependable pollinators.

As *Aspalathus linearis*, rooibos (Figure 131), is a forage plant of *Ceramius clypeatus* and the *Masarina* species, these pollen wasps should be considered as dependable pollinators of this crop plant where it is grown in areas suited to their nesting.

All assemblages from the Western Cape, Namaqualand and the Eastern Cape were characterised by the presence of non-*Apis* bees, Megachilinae (Megachilidae) and Xylocopini (Apidae) or Anthophorini (Apidae), which trip the flowers and carry pollen in the same manner as the *Ceramius* species and, though not restricted to Cape Crotonaceae, are potential pollinators within and beyond the distribution range of the pollen wasps.

The honeybee, *Apis mellifera*, and Eumeninae (Vespidae) visit all three genera but are probably of little importance as pollinators. Honeybees are certainly able to obtain nectar without 'tripping' (opening the keel to expose the anthers and stigma) the flowers.

Caesalpinioideae are generally visited and pollinated principally by solitary bees of several families. We have, however, found unnamed species of *Quartinia* abundantly visiting *Adenolobus pechuelii* (Figure 138), growing in drainage channels in the Namib Desert. Only one of them was present in sufficient numbers at several sites to indicate a possible specialisation. Over most of its distribution *Adenolobus* was visited by bees, mostly anthophorines and anthidiines.



FIGURE 131a, b. *Aspalathus linearis*.



FIGURE 132a, b. *Lebeckia sericea*.

The flowers of Mimosoideae attract visits from a wide range of insects, including diverse wasps and bees. However, there is only one record of a casual visit by a pollen wasp, a single male of *Jugurtia confusa* visiting *Acacia karroo* (Figure 139) in the southeastern Nama-Karoo.

From other areas of the world there are very few records of visits by pollen wasps to Fabaceae. Terry Houston found that in south-

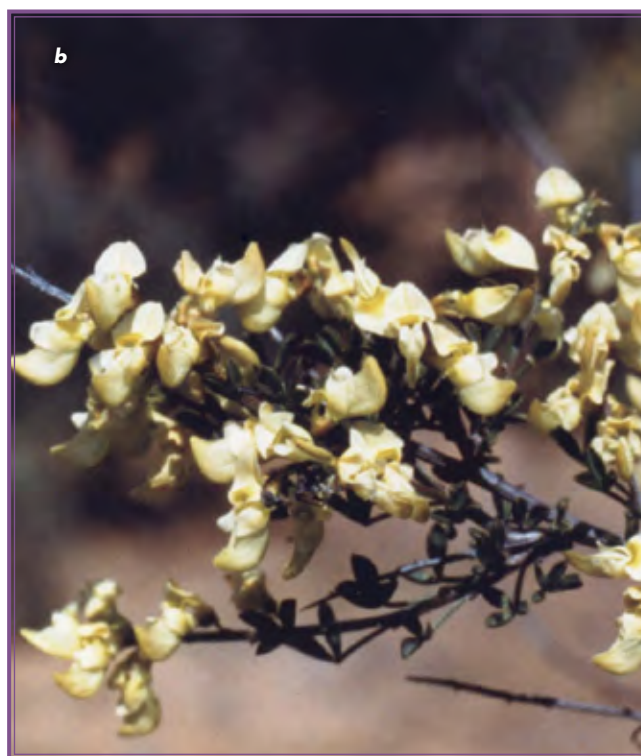


FIGURE 133a, b. *Wiborgia monoptera*.



FIGURE 134. *Aspalathus spinescens*: a. shrub; b. *Ceramius clypeatus* withdrawing from flower; c. *Masarina familiaris* entering flower.

western Australia, one genus of Papilionoideae, *Jacksonia*, is visited for nectar and pollen by *Metaparagia maculata* (Meade-Waldo) (as *Rolandia maculata* in Houston 1995). Recently Volker Mauss (pers. com.) established that in Turkey, *Ceramius palaestinis* (Giordani Soika) forages exclusively on *Trifolium* species (Papilionoideae).

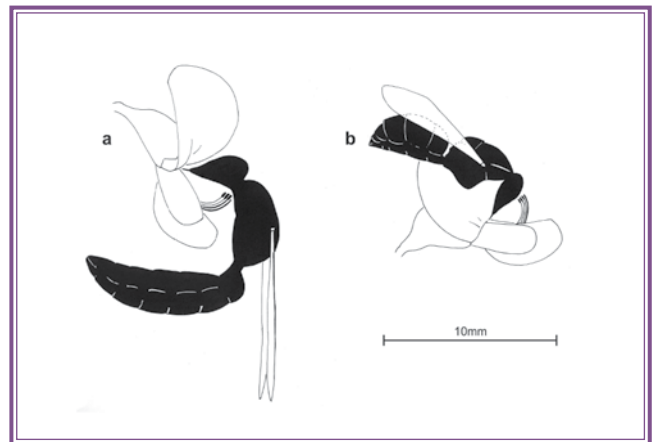


FIGURE 135. a. *Ceramius clypeatus* (legs omitted) in nectar-drinking position on flower of *Aspalathus spinescens*; b. *Masarina familiaris* (legs omitted) in nectar-drinking position on flower of *A. spinescens*.

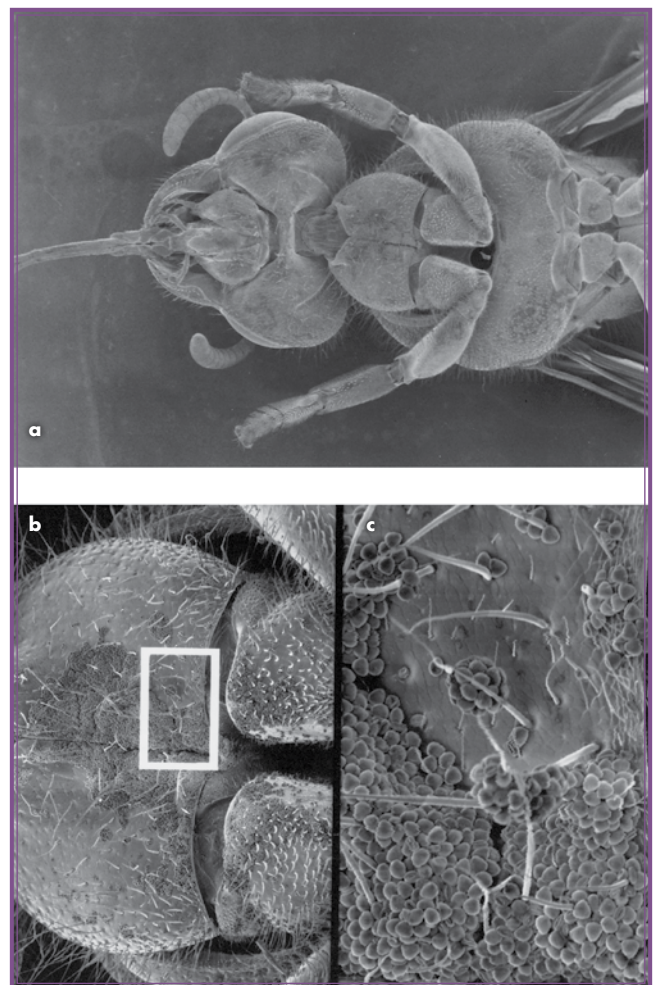


FIGURE 136. *Ceramius clypeatus*: a. ventral view of anterior half of wasp showing area of impact with anthers of *Aspalathus spinescens*; b. prosternum and base of front legs (actual width of boxed area ± 0.7 mm); c. boxed area enlarged.

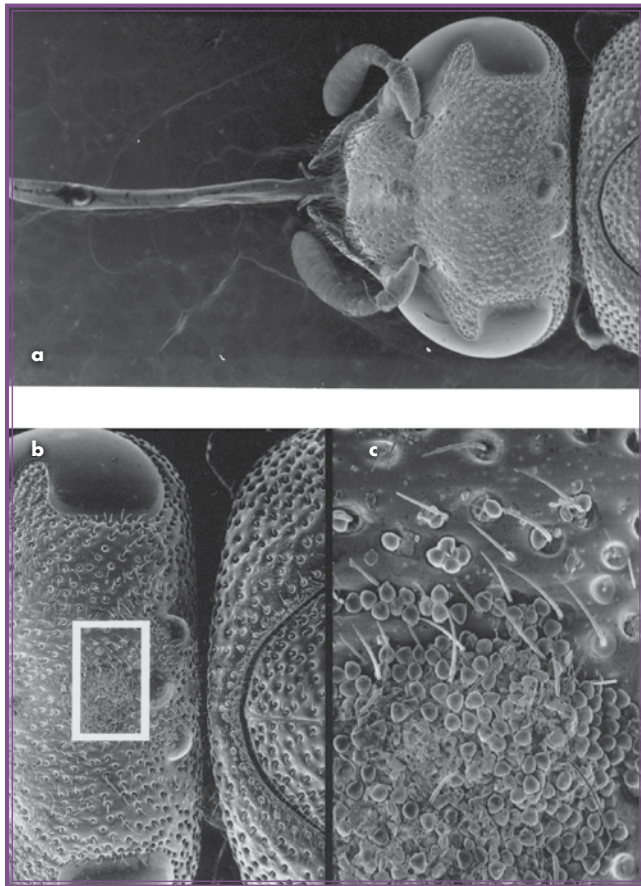


FIGURE 137. *Masarina familiaris*: a. dorsal view of head showing impact with anthers of *Aspalathus spinescens*; b. posterior portion of head (actual width of boxed area ± 0.7 mm); c. boxed area enlarged.



FIGURE 138. *Adenolobus pechuelii*.



FIGURE 139. *Acacia karroo*.

Malvaceae (including Sterculiaceae)

The family Malvaceae is cosmopolitan, with the Sterculioideae most diverse in the tropics and subtropics. Visitation by pollen wasps has been recorded only for southern Africa and here solely for species of *Hermannia* (Sterculioideae), a principally African genus with a few species in America and Australia. Visitation by seven named species of pollen wasps, four species of *Jugurtia* and three species of *Masarina*, was recorded, that is 7% of the named southern African species for which flower-visiting records are available (Appendix 2). Pollen wasp visits to *Hermannia* flowers are frequent and widespread in the west (Figure 140), where *Jugurtia* are expected visitors north of the Orange River and *Masarina* south of the Orange River, but appear to be unusual in the east, only one species having been recorded from *Hermannia* and that at one site only (Figure 140).

Species of *Hermannia* are annual or perennial herbs or small shrubs. The flowers are grouped in terminal pseudoracemes or panicles, are relatively small, yellow, orange, pink, mauve or red and hang down (Figure 141). We have sampled flower visitors to the flowers of 13 identified and some unidentified species. All are visited variously by bees of several families, some of which can be considered to be potential pollinators. Six of the identified and several of the unidentified species, at least, are also visited by pollen wasps, most of which have been recorded from more than one species of *Hermannia*. A pollen wasp visiting these flowers alights on the outside of the corolla, facing downwards (Figure 142), and then curves around to enter the flower. When entering a flower in the pollen-presenting phase, it receives pollen dorsally and, when entering another flower in the pollen-receptive phase, will transfer pollen to the then outwardly directed stigmas. It can therefore be considered as a potential pollinator.

Hermannia modesta (Figures 141e, f), a pink- to red-flowered herbaceous species widespread in southern and western Namibia, is visited abundantly by *Jugurtia alfkni* and *J. mandibulata* from Karasburg in the southeast, northeast to Aranos, west to south of Maltahöhe and northwards to north of Sesfontein in the Kaokoveld and also by *J. damara* from Karibib in thornveld savanna northwest to north of Sesfontein in the Kaokoveld. Visits by the two former species to flowers other than those of *Hermannia* appear to be infrequent and probably casual. The *H. modesta* flowers, like those of most species of *Hermannia*, also attract visits from bees of various families, Andrenidae, Apidae, Halictidae and Megachilidae. However, where they occur, the *Jugurtia* visitors are in fit, behaviour and dependability likely to be the most successful and dependable pollinators.

Of these three species of *Jugurtia*, *J. alfkni* is the most widespread. It was also found visiting red-flowered *Hermannia spinosa* in southeastern Namibia and another red-flowered shrubby *Hermannia*, *H. linearifolia* (Figure 141d), in the south-eastern Nama-Karoo at Vanwyksfontein, Colesberg.

In Namibia, east of the Gamsberg Pass, we found that yellow-flowered *Hermannia comosa*, although growing together with a range of other plants in flower, including mesembs, was being abundantly visited by *Jugurtia confusa*. However, in the Grahamstown district in the southeast where it was found nesting, it obtained pollen for provisioning from mesembs.

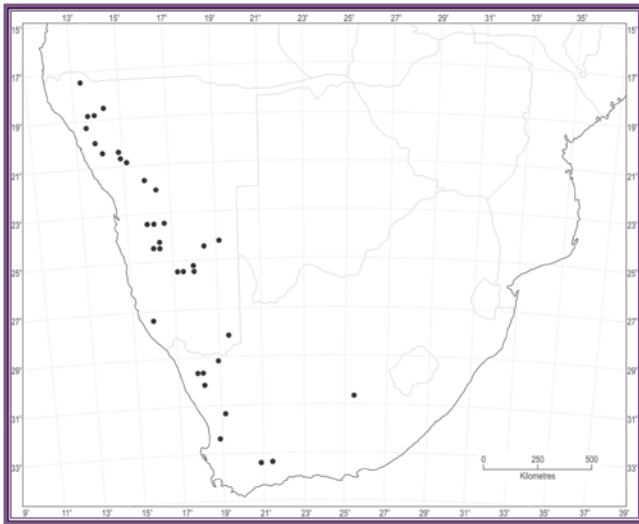


FIGURE 140. Known distribution of pollen wasps visiting *Hermannia* (Sterculiaceae).

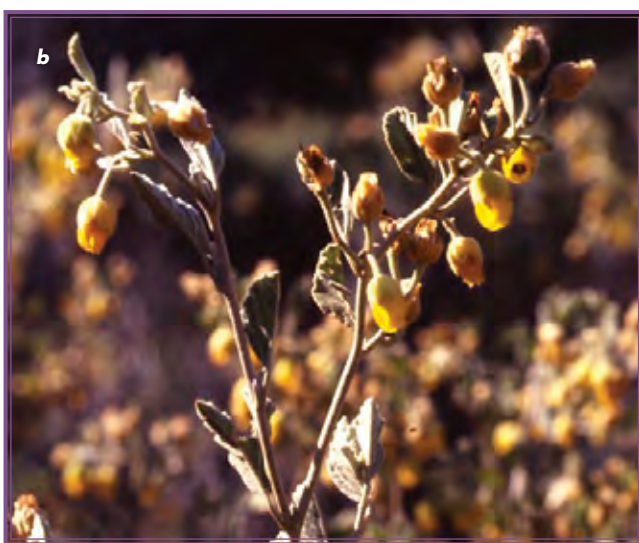


FIGURE 141. Examples of *Hermannia*: a. *H. disermifolia*; b. *H. vestita*; c. *H. engleri*; d. *H. linearifolia*; e, f. *H. modesta*.



Two yellow-flowered shrubby species, *Hermannia disermifolia* (Figure 141a) sampled at several sites in Namaqualand and *H. vestiata* (Figure 141b) sampled in the western Little Karoo, are abundantly visited by *Masarina strucki* together with bees, most commonly Anthophorini. The only other forage plant recorded for this pollen wasp was a third species of *Hermannia*, an orange-flowered herbaceous species of the subgenus *Mahernia* growing in the Olifants River Valley. Also recorded from this species of *Hermannia* was *Masarina mixta*. Nesting was studied in the Kamiesberg where the provision was obtained from *H. disermifolia*. *Masarina strucki* is considered to be the most dependable potential pollinator of the *Hermannia* species that it visits, the bees all being polylectic and *M. mixta* being a casual visitor most commonly associated with, but not restricted to, *Wahlenbergia*.

At Aggeney's, in Bushmanland, an orange-flowered *Hermannia* (*Mahernia*) was found to be visited by a strikingly orange species of *Masarina*, *M. hermanniae*, which visited only these flowers although there was a good selection of other flowers attractive to other pollen wasps.

We sampled low, pink-flowered *Hermannia engleri* (Figure 141c) at several sites north of the Orange River, on the southern and southeastern fringes of the Kalahari and to the southwest of Gibeon, but only at the latter site were pollen wasps included with the complex of bee visitors. At this site, an unidentified species of *Quartinia* was a common visitor but owing to its small size, it is not considered as a potential pollinator.

Geraniaceae

The cosmopolitan family Geraniaceae, well represented in southern Africa, is listed amongst the 10 largest families in Namaqualand-Namib. They are not widely visited by pollen wasps, but

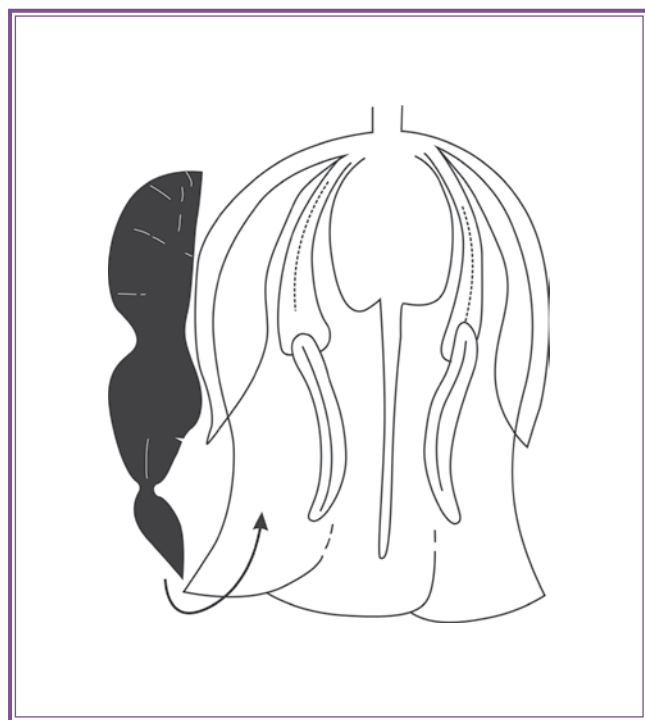


FIGURE 142. Diagrammatic representation of a *Hermannia* flower cut longitudinally with a pollen wasp positioned for entering the flower.

visits to three species of *Pelargonium* and to species of *Sarcocaulon* have been recorded. Included are eight named species of pollen wasps, that is 8% of the named pollen wasp species for which flower-visiting records are available (Appendix 2).

Some 60% of *Pelargonium* species are considered to fall within the bee pollination syndrome within which pollen wasps can be included. To access nectar, visitors to these flowers must be able to reach the nectar at the base of the hypanthium, a slender tube that is decurrent along the pedicel and adnate to it. No pollen wasps have been found to solely visit *Pelargonium*, but it appears that two species, each with at least one other specialisation, may include *Pelargonium* in their specialisations.

Shrubby *Pelargonium klinghardtense* (Figures 143a, b) produces massed white flowers. The opening to the hypanthium is red. In Helskloof in the Richtersveld National Park we have observed the flowers for visitors and on occasion found these to be abundantly visited for nectar by *Jugurtia codoni* and *Masarina mixtoides*, but no other insects. The possession of long tongues makes them admirably suited to obtaining nectar from



FIGURE 143. *Pelargonium*: a, b. *P. klinghardtense*, a. plant, b. flowers; c. *P. capitatum*.

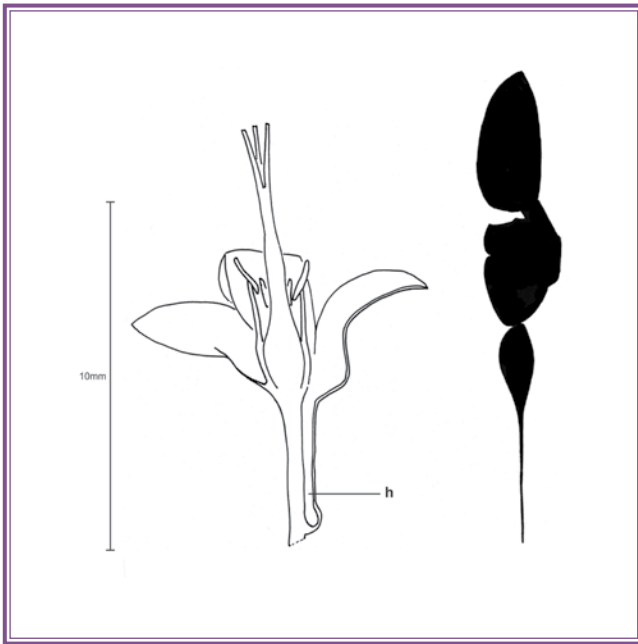


FIGURE 144. Diagrammatic representation of flower of *Pelargonium klinghardtense* and *Masarina mixtoides* to show flower fit; hypanthium labelled 'h'.

the narrow tube (Figure 144), but as their tongues match the tube length they have to press themselves into the flower and in doing so make contact with the anthers when a flower is in the pollen-presenting phase, and with the stigmas when they are in the receptive phase. They are therefore well suited to be pollinators. However, *J. codoni* is an abundant visitor to *Codon* (Boraginaceae), from which it collects both nectar and pollen. *Masarina mixtoides* is not an uncommon visitor to *Zygophyllum* in the same area. Neither species can therefore be considered to be dependable.

In the Graafwater district to the west of Clanwilliam we have found that herbaceous, pink-flowered *Pelargonium capitatum* (Figure 143c) is occasionally visited for nectar by *Celonites wahlenbergiae* and *C. bergenwaliae*, both most commonly found collecting nectar and pollen from *Wahlenbergia* species (Campanulaceae). *Pelargonium capitatum* is also visited by various polyphagous bees, bombyliid flies and lycaenid butterflies.

When sampling flower visitors in the Little Karoo, near Oudtshoorn, Charles Jacot Guillarmod found *Pelargonium myrrhifolium* being most abundantly visited by a pollen wasp, *Celonites capensis*. However, it also received visits from a wide range of polyphagous bees and some eumenine wasps. *Celonites capensis* is the most polyphagous species of *Celonites*, having been recorded by us from flowers of six other families of plants—most frequently and at most sites from Asteraceae.

In an analysis of floral divergence and convergence in *Pelargonium* in southern Africa, Michael Struck found that most of the 208 taxa (species, subspecies and varieties) for which he had flower visitation data, showed bee and long-proboscid hovering fly syndromes (60% and 25% respectively). He estimated that only 7% are pollinated by butterflies, 2–4% by hawkmoths and 1% by birds. Pollen wasps are included in the bee pollination syndrome.



FIGURE 145. *Sarcocaulon patersonii*: a. plant; b, c. flower being visited by *Quartinia poecila*; d. flower being visited by *Apolysis* (Bombyliidae).

The African genus *Sarcocaulon*, concentrated in the Richtersveld and southwestern Namibia, is visited principally by osmiine bees, pollen wasps (several species of *Quartinia*) and by bombilyid flies (Figure 145a–d). The flowers are relatively large, open and regular with five pink or cream, free petals, 15 stamens and five nectaries alternating with the petals.

Boraginaceae (including Hydrophyllaceae)

The cosmopolitan family Boraginaceae as a whole is most diverse in the Mediterranean and in southern Africa, but the sub-family Hydrophyllaceae is most diverse in the dry western areas of North America and is absent from Australia. Pollen wasps have been recorded as visitors to the flowers of Boraginaceae *sensu stricto* in the Mediterranean region, South America and North America. In South Africa, some species, for example the widespread and showy *Anchusa capensis*, attract large numbers and a wide range of bee and wasp families. However, records of visits by pollen wasps to Boraginaceae are very restricted (Figure 146) in distribution and in number of species visited. In North America, 92% of the 13 species of *Pseudomasaris* for which flower-visiting records are available specialise in visiting *Phacelia* and *Eriodictyon* (Hydrophyllaceae). However, in southern Africa only five, 5%, of the named species of pollen wasps for which flower-visiting records are available have been recorded from Boraginaceae (Appendix 2).

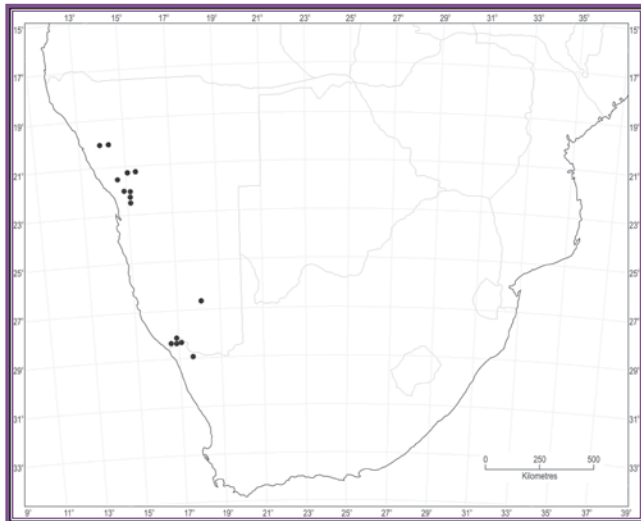


FIGURE 146. Known distribution of pollen wasps visiting Boraginaceae, *Heliotropium tubulosum* to the north and *Codon royenii* (formerly Hydrophyllaceae) to the south.



FIGURE 147. *Codon royenii*: a. plant; b. with *Jugurtia codoni* imbibing nectar; c. with *J. codoni* collecting pollen; d. with *Quartinia* imbibing nectar, collecting pollen and mating; e. with *Xylocopa lugubris* imbibing nectar.

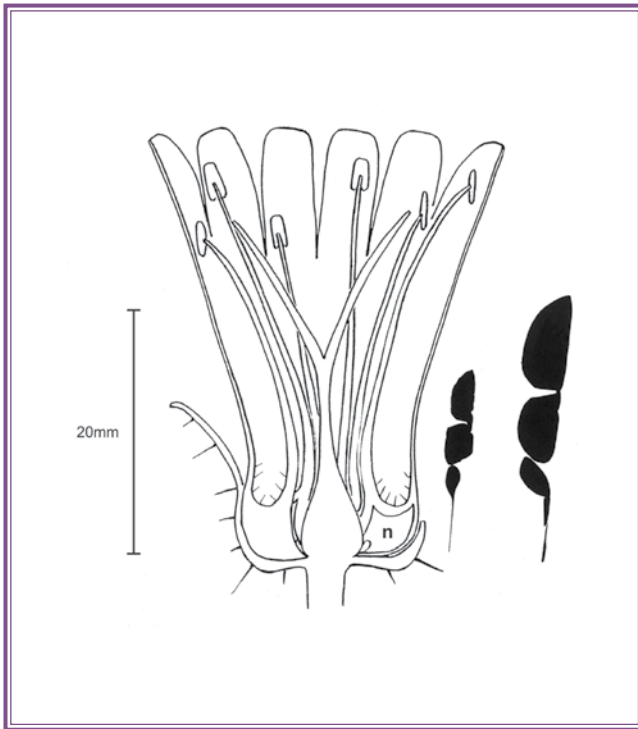


FIGURE 148. Diagrammatic representations of, from left to right, *Codon royenii* flower cut longitudinally, *Jugurtia codoni* (wings and legs omitted) and *Xylocopa lugubris* (wings and legs omitted); nectar chamber indicated by 'n'.

Codon royenii (Hydrophyllaceae) (Figure 147) appears to be the principal forage plant of *Jugurtia codoni* in the Richtersveld and of an as yet unnamed species of *Quartinia* in the Richtersveld, immediately south and north of the Orange River.

The flowers of *Codon royenii*, a spiny herbaceous plant of the arid west, are 35 mm high, erect and campanulate. The many-lobed corolla is white. There are 10–12 stamens. The filaments are attached to the corolla tube about 5 mm from the base and are closely adpressed so that they close off the base of the flower, presumably protecting the nectar from evaporation (Figure 148). When visiting the flower, a pollen wasp alights on the outwardly curved corolla lobes and, when preparing to imbibe nectar, walks down the side of the flower (Figure 147b, d) and inserts its long tongue between the filaments. When collecting pollen, the pollen wasp either reaches over from the corolla or moves across onto a filament and ingests pollen directly from the anther (Figure 147c).

Owing to their small size in relation to the flower, none of the pollen wasp visitors are considered to be a pollinator. The pollinators of this plant in Namaqualand and western Namibia are considered to be *Xylocopa* species (Apidae: Xylocopinae) (Figures 147e, 148).

The discovery of pollen wasp associations with Hydrophyllaceae in southern Africa is of note when considered in relation to the strong association between *Pseudomasaris* and Hydrophyllaceae, a principally American taxon, in western North America.

In northwestern Namibia, *Heliotropium tubulosum* (Heliotropiaceae) (Figure 149), an abundant herbaceous plant in the drainage channels of the central Namib, is frequently visited by two pollen wasps, *Jugurtia namibicola* (Figure 149b) and *Celonites heliotropii* (Figure 149c), both of which have been recorded



FIGURE 149. *Heliotropium tubulosum*: a. plant; b. *H. tubulosum* with *Jugurtia namibicola*; c. *H. tubulosum* with *Celonites heliotropii*.

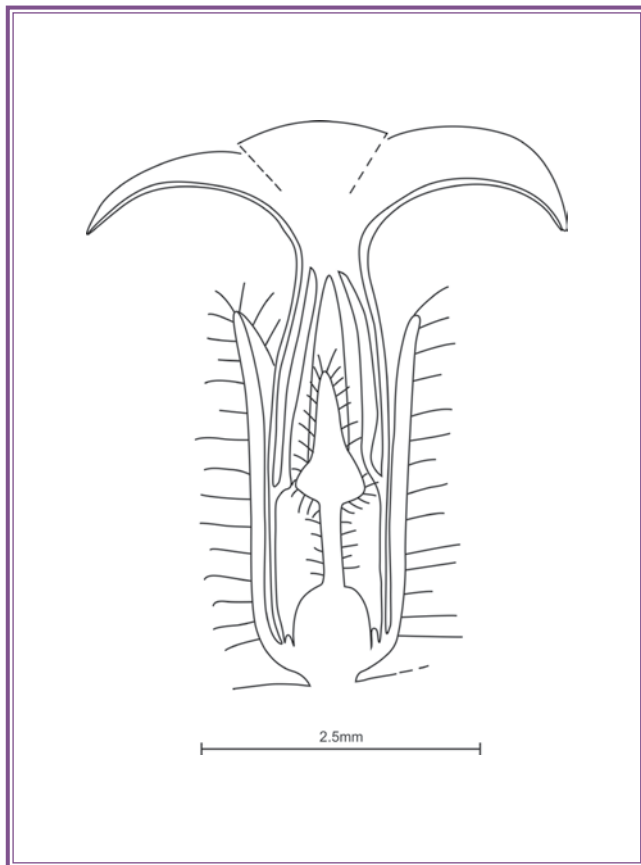


FIGURE 150. *Heliotropium tubulosum*, diagrammatic longitudinal section of flower.

solely from these plants, of which it seems likely that they are pollinators. At some sites they are also visited by butterflies, painted ladies, pierids and lycaenids having been recorded.

The white flowers of *Heliotropium tubulosum* are borne in unilateral cymes. The corolla is tubular, 6 mm high and 1 mm in diameter. The nectaries, situated at the base of the tube, are accessible only to long-tongued insects (Figure 150). The sessile anthers are contained within the tube surrounding the broad base of the hairy stigma, limiting access. When visiting the flowers, the pollen wasps alight on the outwardly curved corolla lobes. When drinking nectar, a pollen wasp reaches into the flowers with its long tongue. Pollination will take place when a nectar-drinking pollen wasp visits a flower in the pollen-presenting stage and later visits a flower with a receptive stigma. Because entry into the flower is restricted, a pollen wasp gathering pollen must reach into a flower with a front leg and scoop or brush it out. The front legs of *Jugurtia namibicola* are especially modified being, for *Jugurtia*, unusually long, gracile and equipped with hooks. Indeed, the fore-legs of *J. namibicola* show similar modifications to those of *Trimeria buyssoni* Br  thes (Masarininae) associated with *Heliotropium* in South America.

The only other recorded visits to Boraginaceae were a single visit in the Richtersveld by an unidentified species of *Quartinia* to *Trichodesma africanum*, which is regularly visited by bees of several families, Apidae, Megachilidae and Halictidae, and a single visit in the Grahamstown area in the southeast by a male *Celonites capensis* to *Ehretia rigida*, which is principally visited and pollinated by carpenter bees, *Xylocopa* spp.

Crassulaceae

The family Crassulaceae is cosmopolitan, excluding Australia and the western Pacific. It is listed as one of the largest families in the Karoo-Namib, but the flowers are generally not visited by pollen wasps. Only two, 2%, of the named species for which flower-visiting records are available visit flowers of Crassulaceae (Appendix 2). For other regions, the only records seem to be that of *Celonites abbreviatus* (Villiers) visiting *Sedum* in southern Germany.



FIGURE 151. Crassulaceae visited by pollen wasps: a. *Tylecodon hallii*, plant; b. *Masarina tylecodoni* entering flower of *T. hallii*; c. *Crassula dichotoma*.

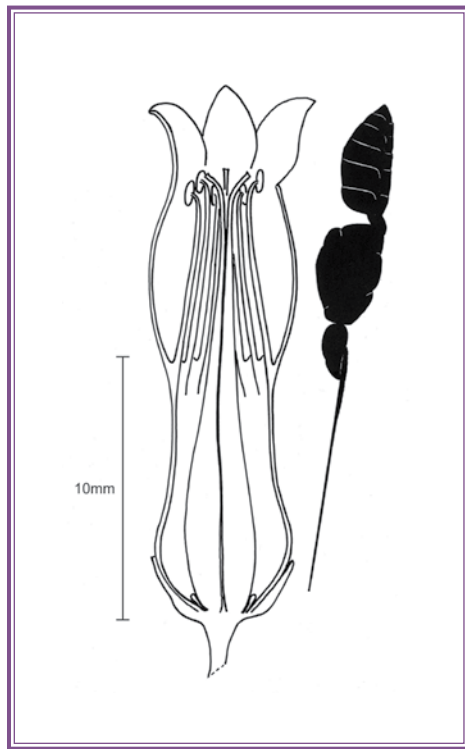


FIGURE 152. Diagrammatic representations of *Tylecodon hallii* flower cut longitudinally and of *Masarina tylecodoni* (wings and legs omitted).

Tylecodon hallii appears to be visited solely by *Masarina tylecodoni*, which has been shown to be morphologically and behaviourally suited to pollinating it (Figures 151, 152). Bird and fly pollination have been observed for other species of *Tylecodon*, *T. paniculatus* (Figure 153a) and *T. cacalioides* (Figure 153b) respectively, morphologically very different from *T. hallii*. The latter is narrowly endemic, being known solely from the northern Richtersveld and an adjacent area in Namibia, where it grows on rocky spurs, characteristically quartzite outcrops. It is a small, compact succulent tree that reaches a height of approximately 30 cm. It has a grey to almost black trunk and narrow, rough-surfaced, succulent leaves, and holds aloft an abundance of sticky, yellow, erect, deeply campanulate (bell-shaped) flowers about 22 mm high, which are clearly not designed to attract birds like the flowers of the botterboom, *T. paniculatus*, with its striking red inflorescence stems.

The flowers of *Tylecodon hallii* offer a rich reward of nectar and pollen. The nectar is not readily accessible, being hidden beneath the closely adpressed filaments attached to the corolla just above its 'waist' (Figure 152). When visiting a flower for nectar, *Masarina tylecodoni*, characteristically of pollen wasps, alights on the outwardly curved petal lobes and enters between the corolla and the staminal filaments (Figure 151b) which, being closely adpressed, form a barrier to the pollen wasp. The insect then inserts its long tongue between two filaments to reach the nectar in the base of the flower. In forcing its way into the flower, *M. tylecodoni* pushes against the anthers and, if the anthers are ripe, receives a load of pollen on its back. When it leaves a flower in the pollen-presenting phase and then enters a flower with outwardly curved receptive stigmas it will wipe the pollen off its back onto one or more of the stigmas. It is therefore well suited to being a pollinator.

Pollen deliberately collected is ingested directly from the anthers and is not gathered by brushing off the pollen received when

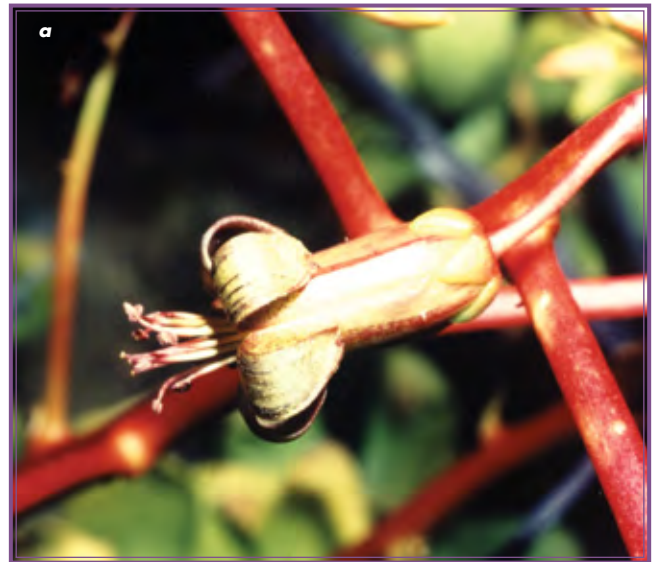


FIGURE 153. Examples of *Tylecodon* species not visited by pollen wasps a. *T. paniculatus*, bird-pollinated; b. *T. cacalioides*, fly-pollinated.

collecting nectar, so that pollen remains available for pollination.

The site at which we made this study is in the hilly area to the west of the Koeroegabvlakte, in the Richtersveld National Park. In September 1995 and again in 1997, visitors to flowers were sampled on the banks of the gravelly drainage channels and the associated rocky slopes. It was found that 28 out of 32 species of flowers belonging to 13 families were being visited, variously, by bees and wasps, including pollen wasps. In both years *Tylecodon hallii* was visited solely by *Masarina tylecodoni* and this pollen wasp visited only flowers of that plant, indicating that there may be a close mutualistic relationship between the two organisms. It is possible that *M. tylecodoni* may visit other species of *Tylecodon*, as pollen wasps, though often restricted to a small number of closely related plants, have never been found to be associated with a single species of plant. It would, however, still be a very dependable pollinator of *T. hallii* as this species of *Tylecodon* is the first to come into flower in the Richtersveld.

The only other member of the Crassulaceae recorded as receiving visits from a pollen wasp is *Crassula dichotoma* (Figure 151c), an annual herb found together with *Wahlenbergia* in sandy areas in the southwest. It bears erect, campanulate flowers. At Clanwilliam we have found it receiving nectar collection visits from *Celonites wahlenbergiae*, a species closely associated with *Wahlenbergia*, although a visitor to other flowers as well.

Neuradaceae

The family Neuradaceae is found in semi-arid to arid areas in southern Africa, and North Africa eastwards to India. Visits by pollen wasps have been recorded solely from southern Africa. The genera *Grielum* and *Neuradopsis* are endemic to western southern Africa. All are low herbs with shallowly campanulate yellow flowers (Figure 154). These are visited most commonly by bees of several families, Apidae, Megachilidae, Halictidae and in particular Colletidae (Figure 154c). However, visits from three named pollen wasps, all species of *Quartinia*, *Q. poecila* (Figure 154b), *Q. propinqua* and *Q. refugicola*, have been recorded in southwestern desertic Namibia (Appendix 2). Only *Q. poecila* is a very abundant visitor to *Grielum*. In the Sperrgebiet and the southwestern desert fringe it is a common visitor to *G. sinuatum*, but along the west coast from Hondeklip Bay in the south to Swakopmund in the north it is an abundant visitor to mesembs and Asteraceae. *Quartinia propinqua* is an occasional visitor to *G. grandiflorum* in the Richtersveld but is an abundant and widespread visitor to Asteraceae, from southeastern Namaqualand northwards through western Namibia. *Quartinia refugicola* is similarly an abundant visitor to Asteraceae and an occasional visitor to *Grielum* but is known only from southwestern desertic Namibia where it nests in sand trapped in snail shells.



FIGURE 154a–d. *Grielum sinuatum*: a. plant; b. flower being visited by *Quartinia poecila*; c. flower being visited by a colletid bee, *Scrapper* sp.; d. flower being visited by a bee-fly, *Megapalpus* sp.

Amaranthaceae

The family Amaranthaceae is mainly tropical in distribution and is most diverse in America and Africa. It forms a notable component of the vegetation of northern Namaqualand and Namibia. Preliminary palynological evidence suggests that they were a previously predominant element before Aizoaceae: Mesembryanthema took over in the early Holocene. Several species are very attractive to a wide range of wasps and bees but only two species of pollen wasps have been recorded making occasional casual visits, *Jugurtia codoni* to *Hermbstaedia glauca* in the Richtersveld and *Ceramius damarinus* to *H. odorata* in north-western Namibia (Appendix 2).

Visits by pollen wasps have been recorded solely from southern Africa.

Acanthaceae

The cosmopolitan family Acanthaceae is most abundant in the tropics and subtropics. It is one of the 10 largest plant families in the Damaraland-Kaokoveld. Though less diverse in the Nama-Karoo, it is widespread. However, only one pollen wasp, *Ceramius lichtensteinii* which specialises in mesembs throughout its range, has been recorded from a species of Acanthaceae, *Blepharis capensis*, at two widely separated sites in the south-east, near Grahamstown and Waterford. Flowers of this plant are commonly visited and pollinated by bees of several families, Apidae, Megachilidae and Halictidae.

Lamiaceae

The cosmopolitan family Lamiaceae is amongst the plants favoured by pollen wasps in the Palearctic and is casually visited in North America. It occurs throughout southern Africa but is most species diverse in the east. The flowers of 10 species that we sampled for flower visitors are all visited by bees of various families, mostly Megachilidae but also Apidae and Halictidae, and in the east also by long-tongued flies. Only *Ocimum americanum*, in northwestern Namibia on the desert fringe where casual visiting by pollen wasps is at its highest, received casual visits from pollen wasps, *Ceramius damarinus* and *Jugurtia alkfeni*.

Nyctaginaceae

The family Nyctaginaceae is chiefly American with a few species in southern Africa, India, the Mascarene Islands and the Pacific Islands. No pollen wasps are known to specialise in visiting Nyctaginaceae. However, two pollen wasps, *Celonites michaelsoni* which specialises in visiting Aptosimeae and an unnamed species of *Quartinia* that has been recorded from flowers of eight plant families, were amongst the assemblage of wasps and bees visiting small white flowers of *Boerhavia deserticola* near Palm on the desert fringe in northwestern Namibia.

Plumbaginaceae

The cosmopolitan family Plumbaginaceae is most species diverse in the Mediterranean region and the Middle East. It is represented in southern Africa by three genera, *Plumbago* with slender tubular flowers, *Dyerophytum* with more funnel-shaped flowers and *Limonium* with petals separate or only fused for a short distance. The flowers of *Limonium* are visited by wasps and bees, those of the other two genera by butterflies. Generally *Limonium* does not appear to be visited by pollen wasps, but *Celonites promontorii*, specialising in Asteraceae, and two unnamed species of *Quartinia*, specialising in mesembs, were recorded from *Limonium* east-northeast of Ceres in the southwest and a further species of *Quartinia* was found to be foraging on *L. scabrum* (Figure 155) together with mesembs on the south coast near Mossel Bay.

Euphorbiaceae

The cosmopolitan family Euphorbiaceae is amongst the largest families in the southern Karoo, Namaqualand-Namib and Damaraland-Kaokoveld. The flowers are not visited by pollen wasps, but nectar collection by *Priscomasaris namibiensis* from the extrafloral nectaries of a herb, *Euphorbia glanduligera*, was observed near Büllsport where this wasp was otherwise



FIGURE 155a, b. *Limeum scabrum*.

abundantly visiting *Limeum* and *Gisekia* (Molluginaceae), its more usual forage plants, for pollen and nectar.

Brassicaceae (including Capparaceae)

The family Brassicaceae as a whole is cosmopolitan, but the 'Capparaceae' are restricted to warm and tropical countries. *Cleome* (formerly in Capparaceae), a widespread genus in southern Africa, forms a common and showy component of flower communities south of the Orange River in the west and northwards through Namibia. We have recorded occasional visits to *Cleome paxii* (Figure 156) by *Jugurtia koeroegabensis* and *Quartinia propinqua* in the northern Richtersveld and to *C. elegantissima* by *J. alkfeni* in northwestern Namibia. These visits were probably casual. The regular visitors and likely pollinators of *Cleome* are bees, most notably of the tribes Anthophorini, Xylocopini and Megachilini.

Vahliaceae

The monogeneric family Vahliaceae is native to Africa and tropical to subtropical Asia. *Vahlia* is represented by three species in southern Africa. We have sampled the small, yellow flowers of *V. capensis* at sites from Augrabies northwards to the Kuiseb. Visits by bees of several families were recorded but only a single visit by a pollen wasp, *Quartinia propinqua*, a species widely associated with Asteraceae.

FIGURE 156a, b. *Cleome paxii*.

MONOCOTYLEDONS

Asphodelaceae

The family Asphodelaceae is restricted to the Old World. In southern Africa, Asphodelaceae are known to be visited by a diversity of bees but visits from pollen wasps are unusual, only two species having been recorded from these plants. *Aloe striata*, which was observed for flower visitors over a two-week period on the farm Tierberg near Prince Albert, was repeatedly visited by *Quartinia antigone*, for which no other flower-visiting records are known.

Flowers of at least two species of white-flowered *Trachyandra* are visited by pollen wasps. One, *T. divaricata* (Figure 157) is

FIGURE 157a, b. *Trachyandra divaricata*.

visited relatively abundantly on the southwest coast by *Quartinia bonaespei*, a nester in snail shells, and *T. muricata* is visited occasionally by *Jugurtia braunsi* in the Olifants River Valley. Both also visit mesembs, which are the flowers of choice of the latter in Namaqualand and the Olifants River Valley.

Iridaceae

The family Iridaceae is cosmopolitan but is most diverse in southern Africa. Visits by pollen wasps to Iridaceae are unusual but, interestingly, we found flowers of *Ferraria variabilis* (Figure 158a) receiving visits from *Jugurtia koeroegabensis* in the Richtersveld, and flowers of *Ferraria kamiesbergensis* (Figure 158b) receiving visits from *Celonites capensis* in the Kamiesberg. Both have greenish yellow flowers that offer abundant nectar and attract repeated visits by these pollen wasps.

The pollen wasps are relatively polyphagous, *Celonites capensis* having been recorded from flowers of seven families but most commonly from Asteraceae and Geraniaceae and *Jugurtia koeroegabensis* having been recorded from flowers of five families but most commonly from *Peliostomum* (Aptosimeae).

Until recently *Ferraria* was generally considered to be attractive only to flies or flies and small beetles, but Peter Bernhardt and Peter Goldblatt have now confirmed our observations that *Ferraria* does attract visits from Vespidae. Their new records are for *F. divaricata* and *F. variabilis* being visited by polyphagous eumenine wasps.

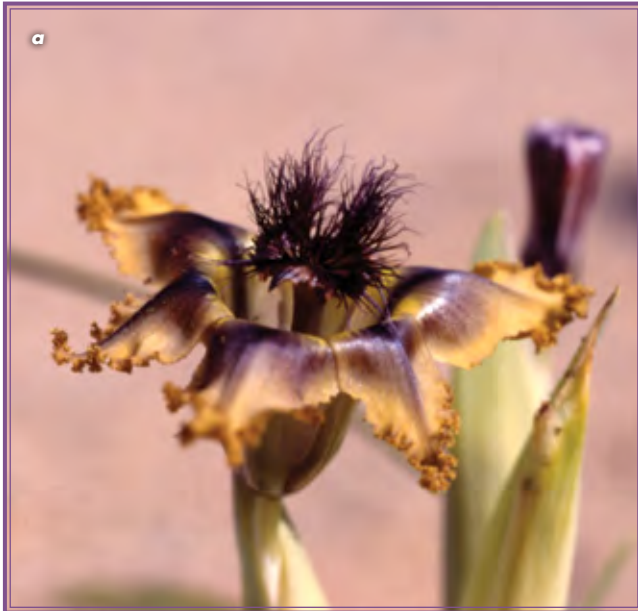


FIGURE 158. *Ferraria*: a. *F. variabilis*, Richtersveld; b. *F. kamiesbergensis*, Kamieskroon.

Pollen wasps as pollinators of the flowers they visit

The above survey of flowers visited by pollen wasps and the potential of the pollen wasps as pollinators of the flowers they visit, indicates that:

- **Asteraceae.** Throughout the semi-arid to arid areas of southern Africa pollen wasps, in particular those specialising in visiting composites, should be considered as potential pollinators, but not sole pollinators, of a wide range of taxa.
- **Scrophulariaceae.** Throughout the semi-arid to arid areas of southern Africa where Aptosimeae are present, specialist pollen wasps, mostly of the genus *Celonites*, should be considered to be their principal and dependable pollinators. Though occasional visitors to other taxa of Scrophulariaceae, pollen wasps are of little or no importance as potential pollinators of these flowers.
- **Campanulaceae.** In southwestern South Africa specialist pollen wasps are probably the most important and most dependable pollinators of deeply campanulate-flowered *Wahlenbergia* and *Microcodon* (Campanuloideae). However, although they visit some stellate-flowered *Wahlenbergia*, they are not potential pollinators of these flowers. In southeastern Namaqualand, a species of pollen wasp, *Celonites lobeliae*, together with a small carpenter bee, is a possible potential pollinator of *Lobelia linearis* (Lobelioideae).
- **Zygophyllaceae.** From the Richtersveld northwards through western Namibia, pollen wasps are expected visitors to *Zygophyllum* and are probably amongst their potential pollinators but it is probable that they are only of possible importance to *Z. simplex*.
- **Fabaceae.** In western South Africa specialist pollen wasps are amongst the potential pollinators of Cape Crotalariaeae, including cultivated *Aspalathus linearis*, rooibos, and where they occur together, the specialist pollen wasps are dependable.
- **Malvaceae.** From the western Little Karoo westwards to the Olifants River Valley and northwards through Namaqualand and Namibia to the Kunene River, specialist pollen wasps are amongst the most important potential pollinators of some species of *Hermannia*.
- **Geraniaceae.** Pollen wasps are not generally members of assemblages of visitors to Geraniaceae, but it is possible that they may be of some importance as potential pollinators of some species of *Pelargonium* and *Sarcocaulon*.
- **Boraginaceae.** Specialist pollen wasps are associated with *Heliotropium tubulosum* in the desertic areas of northern Namibia and with *Codon royenii* in the Richtersveld south and north of the Orange River. It seems likely that *Jugurtia namibicola* and *Celonites heliotropii* are the most important and most dependable pollinators of *H. tubulosum*. However, owing to their relatively small size, the pollen wasps visiting *Codon royenii*, which is pollinated by *Xylocopa*, large carpenter bees, are not suited to pollinating these flowers.
- **Crassulaceae.** A specialist pollen wasp, *Masarina tyledoni*, is the only known potential pollinator of *Tylecodon hallii*. Both are narrowly endemic to a small area of the Richtersveld south and north of the Orange River.
- **Aizoaceae: Mesembryanthema.** In areas south and north of the Orange River where pollen wasps, in particular those specialising in visiting mesembs, are present together with Aizoaceae: Mesembryanthema, they should be considered as potential pollinators, but not the sole pollinators, of a wide range of taxa with carpet, cone and recess flowers, but probably not cup flowers.
- **Aizoaceae: non-Mesembryanthema and Molluginaceae.** In areas in northern Namaqualand and in the semi-arid to arid areas of Namibia where pollen wasps are present together with Aizoaceae: non-Mesembryanthema and Molluginaceae, they should be considered as potential pollinators, but not the sole pollinators, of the flowers of the taxa they visit.

- **Neuradaceae.** It is considered possible that some pollen wasps, species of *Quartinia*, may be amongst the potential pollinators of *Grielum* in southwestern desertic Namibia.
- **Amaranthaceae, Acanthaceae, Nyctaginaceae, Brassicaceae and Vahliaceae.** Members of these families receive casual visits from pollen wasps but no pollen wasps have been found to be of any importance as potential pollinators of these plants.
- **Plumbaginaceae.** *Limonium* is visited by pollen wasps in the southwestern Western Cape. Along the southern coast it is likely that species of *Quartinia* are at times and in some places of note as potential pollinators.
- **Asphodelaceae.** *Trachyandra* growing amongst coastal dunes in the southwest are attractive to pollen wasps, which have the potential to be pollinators of the flowers. At Tierberg near Prince Albert in the southern Karoo *Aloe striata* was abundantly visited over a period of a few days solely by *Quartinia antigone*, which was considered to have the potential to pollinate the flowers. This was an isolated incidence, suggesting only that at times and in some places it is possible that pollen wasps may be potential pollinators of some species of *Aloe*.
- **Iridaceae.** Pollen wasps are not generally amongst the visitors to Iridaceae, but it is of interest that pollen wasps have been found to visit species of *Ferraria* with greenish yellow flowers producing abundant nectar. These flowers, unlike those of other *Ferraria* species which are fly-pollinated and do not attract wasps, are also visited by eumenines and it has been suggested that they may be pollinated by the wasp visitors.

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Impact of land use practices on pollen wasps

Pollen wasps, like solitary bees, are particularly sensitive to habitat changes. All pollen wasps, like bees, require the presence of their forage plants, suitable nesting sites and other resources necessary for nesting, for instance clean water for nesters in nonfriable clayey soils. As pollen wasps are oligophagous or narrowly polyphagous, a very limited range of plants is acceptable to them, as to oligophagous bees. Whereas many bees can forage on flowers of alien plants, including some crop plants, no pollen wasps have been found foraging on the flowers of alien plants.

Obviously, the ever increasing space required for building, mining and roads, presents major localised threats to almost all organisms for which the areas involved are their habitats. Most farming activities, carried out without taking into account the habitat requirements of organisms both large and small, have the potential to cause widespread loss of species.

If one considers that not only are pollen wasps sensitive to habitat change but that many have very limited distribution ranges, it is obvious that they are very vulnerable to extinction. As many pollen wasps are the sole or most dependable pollinators of the flowers they visit, it is clear that loss of species would have a cascade effect. Clearly the most threatened species are those that are narrowly endemic. Most species with restricted distributions are found in the southwest of southern Africa, the most developed part of southern Africa.

Ground-nesting pollen wasps, *Priscomasaris*, *Ceramius*, *Jugurtia*, some *Masarina*, *Celonites* and *Quartinia* species, like other ground-nesting wasps and bees, require areas of undisturbed exposed ground for positioning of nests and are therefore unable to nest where the soil is subject to ploughing, excessive trampling or other disturbance. In addition, species nesting in nonfriable soil, including pollen wasps of the genera *Priscomasaris* and *Ceramius*, and some species of *Jugurtia* and *Masarina*, require a source of unpolluted water for burrow excavation and nest construction. Nesting success of those pollen wasps, for example some *Celonites* species, that construct nests on plants, like the nesting success of other wasps and bees nesting in this manner, may be adversely affected by unnaturally heavy browsing.

Naturally occurring water sources are springs, rivers, temporary pans and temporary rainwater puddles. These are supplemented by boreholes, dams and furrows. Dams range from small impoundments of water held by earthen banks, used principally for watering stock, to major dams for supply of water for irrigation of crops and to dwellings, factories, mines etc. In all instances water becomes unavailable when it is heavily polluted by stock coming to drink or by effluents. Only species that alight on the water surface are able to make use of water sources with steep sides.

Localised large-scale flooding of land resulting from the damming of rivers clearly results in localised extirpation of whole communities of organisms, including pollen wasps, wasps and bees. The availability of water for nesters on the fringes of large water bodies is dependent on the nature of the terrain, inlets with gently sloping shores and still water being more suited to aculeate wasps and bees that collect water or mud than are

shores subject to wavelet action. Steep-sided water bodies are unavailable to most species. Furthermore, the water in irrigation canals with steep concreted sides and rapidly flowing water is not available to aculeate wasps and bees and such canals therefore do not represent additional water sources.

Crop production results in a complete change in the available resources. Soil structure and plant cover of cultivated land are clearly different from those of uncultivated land. Where crops are farmed under irrigation, water sources are modified by changing water flow of rivers and by damming and furrow construction. The impact that cultivation will have on total species diversity clearly depends upon how extensive the cultivation is and how widespread the affected species are.

Owing to the availability of water, areas most suited to large-scale cultivation are the same areas that are particularly suited to intensive nesting by pollen wasps, indeed by a wide range of aculeate wasps and bees. Ploughing, clearing of vegetation and replacement with a limited range of crop plants, most of which are alien, and application of 'artificial out of season rain' result in localised extermination of entire communities. The extent of the cultivated areas will govern the overall extent of this loss. Where there is rapid expansion of land under cultivation and where there is a high incidence of endemism, as with the pollen wasps, multiple species loss is anticipated.

Pollen wasps forage beyond the limits of their nesting sites. It is therefore possible to have a situation where, in an intensively cultivated area, suitable nesting sites for some species may remain on the fringes of these areas but that the forage plants are no longer available. Unlike some megachilid and anthophorid bees, which are able to forage on alien leguminous crops, masarine wasps do not transfer to alien crop plants.

When lands are left fallow or abandoned, pioneer plants come in. Initially a limited range of annuals predominate, often forming almost pure stands. These annuals may be alien weed species or species that are present but uncommon in the species diverse communities of the surrounding undisturbed areas. The result is an increase in population size of the insect species associated with these plants and a decrease in species diversity as compared with that of the surrounding areas. This effect is strikingly demonstrated by the wasp and bee species associated with complexes of sympatrically occurring *Wahlenbergia* species to the west of the Olifants River Valley. A number of species with deep flowers are principally visited by several species of pollen wasps, whereas a shallow-flowered species, *W. annularis*, is principally visited by two species of melittid bees. Areas where the deep-flowered *Wahlenbergia* species were formerly abundant and *W. annularis* was uncommon have been cultivated and then allowed to go fallow. In these areas *W. annularis* is now the dominant plant, which has resulted in the masarines having been displaced and the melittids having become unnaturally abundant.

Winter-rainfall area

The western Little Karoo, lying between the southern coastal mountains and the southern escarpment, is largely farmed for deciduous fruit, with the Oudtshoorn area being the centre of ostrich farming. The ostriches, in the main, are pastured on lucerne lands in the irrigable river valleys. As the river valleys



FIGURE 159. Heavily cultivated area south of the Olifants River Mountains.

are the areas most suited to nesting by ground nesters, narrowly endemic species such as *Ceramius jacoti* have ever reduced nesting areas not only as a result of cultivation but, where there are ostriches, also as a result of severe trampling of the ground.

To the south of the Olifants River Mountains within the Fynbos Biome only small pockets of indigenous vegetation remain, almost all the land between the mountains that can be ploughed having been given over to agriculture, mainly to the production of wheat (Figure 159), grapes and deciduous fruit. Only small isolated pockets of unploughed land remain as refuges. River valleys are to a large degree infested with alien weed species, most notably Australian *Acacia* species and *Sesbania*. Mountain slopes in some areas have been planted with pines and are generally increasingly subject to invasion by alien weed species. Clearly in the area from the Olifants River Mountains to the Cape Peninsula the future for pollen wasps is bleak.

The area north of the Olifants River Mountains, west of the western escarpment, can be divided into two regions, that to the south stretching from the Cederberg to the sea and including the Olifants River Valley and that to the north known as Namaqualand stretching from Vanrhynsdorp in the south to the Orange River in the north. The Olifants River rises in fynbos to the south in the Citrusdal district and passes through a mosaic of fynbos and karroid scrub on its way north and west to the sea. The river is strong flowing and perennial, making the area ideally suited to irrigation farming. By 1732, European farmers were well established along the Olifants River as far north as its confluence with the Doorn River. With the construction of the Bulshoek Dam in 1922, the Clanwilliam Dam in the 1930s and a system of canals, the valley has been intensively developed (Figure 160) for the large-scale production of citrus fruit, deciduous fruit, vegetables and vines. In addition, in the Vredendal district there are more than 800 active land owners involved in the state's irrigation scheme and the largest co-operative wine cellar in the southern hemisphere. To the west of the Olifants River, the hills are in dry fynbos and the coastal plain in sandveld fynbos. There is widespread large-scale farming, notably of rooibos tea, cereals and potatoes, resulting in an ever increasing removal of forage plants and nesting sites (Figures 161, 162). Strip farming, once favoured to the north and west of Clanwilliam, at least offered refuges but this method is giving way to the more economically productive total destruction.

Namaqualand stretches from Vanrhynsdorp in the south to the Orange River in the north. It lies entirely in the Succulent Karoo.



FIGURE 160. Irrigation farming in the Olifants River Valley.



FIGURE 161. Extensive cultivation west of the Olifants River Valley, lands divided up with parallel rows of saltbush.



FIGURE 162. Potato-growing in the sandveld to the west of the Olifants River Valley.

It can be divided into four subregions, the Knersvlakte in the south, Namaqualand Klipkoppe to the north, the Richtersveld in the extreme northwest and extending across the Orange River into the area known as the Sperrgebiet, and the Sandveld of the coastal plain. Namaqualand is principally given over to small stock farming with, to the south of Springbok, opportunistic small-scale grain production relying on winter rain. In many areas the ground has been severely damaged as a result of trampling by small stock. Furthermore, the species composition of the vegetation has been seriously affected, there having been a marked reduction in species diversity and the dominant plant now being *Galenia africana* (Aizoaceae: non-Mesembryanthema). As small stock do not utilise this pioneer plant, it has increased and is now dominant in much of Namaqualand and the other semi-arid winter-rainfall areas of South Africa.

Summer-rainfall area

The principal summer-rainfall areas in which pollen wasps are present are the Nama-Karoo, those areas of Savanna fringing the Nama-Karoo and the Namib and Kalahari Deserts.

The greater part of the Nama-Karoo supports a profitable small stock industry that is mainly based on natural pastures.

The impact of small stock farming on the environment is variable. Variations in rainfall and vegetation dictate different choices of breed of goats or sheep and the number of head that can be supported. Furthermore, which animals are run has a profound effect upon which plants are fed upon. Whether or not rotation is practised and what pattern of rotation is followed, further affects the vegetation. For example, in the southeastern Nama-Karoo long-term experimental grazing treatments have shown that on plots grazed only in summer, there is a marked increase in the dwarf shrub and decrease in the grass element, whereas on plots grazed in the winter there is a marked decrease in the dwarf shrub element and increase in the grass element (Figure 163). Furthermore, drought may cause high mortality of some species that, in the absence of continuous grazing, would re-establish after good rains. However, under current grazing practices, local extinction of species after drought is not uncommon, resulting in possibly irreversible changes in vegetation structure and composition. Many studies have aimed at assessing grazing capacities, especially since the launching of the National Grazing Strategy in 1985. Nearly all studies reflect excessive stocking rates, which together with injudicious veld management, is the cause of widespread degradation. The number, nature of and distribution of watering points is also variable and brings about different patterns of soil trampling. Clearly such variations in farming practice have a profound effect on the resources available to pollen wasps and the other aculeate wasps and bees of the communities of which they are a part.

In the south, natural pastures are supplemented to a limited but ever increasing extent by the cultivation of lucerne pastures and lucerne hay. Lucerne production is restricted almost entirely to the generally very limited irrigable areas along watercourses, which are the favoured nesting areas of *Ceramius* and *Jugurtia* species and the only areas in which sizeable nesting aggregations of some thousands of nests develop. Ploughing such land clearly has a devastating effect on populations of these pollen wasps. Smaller aggregations do build up in association with farm dams and irrigation furrows, but are vulnerable to trampling. Furthermore, the water is liable to pollution by stock, making it unacceptable to those pollen wasps that require clean water. Changes in farming practice may result in the disappearance of the structures that hold the water or in their sudden total removal.

The Savanna is largely used for cattle ranching and, to a lesser degree, small stock farming. Again the number, nature of and distribution of watering points is variable and brings about different patterns of soil trampling (Figure 164). Clearly such variations in farming practice have a profound effect on the resources available to pollen wasps and the other aculeate wasps and bees of the communities of which they are a part.

Within the last ten years there has been a significant change from stock farming to game farming on many farms in the Nama-Karoo and Savanna. This has resulted in changes in the partitioning of the land and most notably in changes in grazing



FIGURE 163. Grootfontein, eastern Nama-Karoo, showing two plots, one grazed only in winter and the other grazed only in summer.



FIGURE 164. Overgrazed and heavily trampled area south-west of Palmwag, northwestern Namibia.



FIGURE 165. Overgrazed land in the Kaokoveld, pioneer groundcover solely *Tribulus*.

and browsing patterns. Studies of these effects are still in their preliminary phases.

Apart from the area principally to the south of the Lüderitz–Aus road, the Namib Desert lies in the summer-rainfall area. Collecting of pollen wasps over the last 10 years, principally by us, has demonstrated that it is more species diverse than previously thought. Most pollen wasp activity in this very arid area is limited to the coast, which receives frequent heavy moisture-bearing fogs, and to drainage channels associated with the ephemeral rivers that run across the desert from the east, these two situations being most dependably productive of flowering plants. Apart from times of unusually high rainfall, inland there is no surface water except in areas where it is trapped by rocks.

Along drainage channels, pollen wasps penetrate the desert from the east and from the west, there being an interdigitation of inland and coastal species. In the dune fields where plants occur pollen wasps are also found. For example, *Trianthema hereroensis* (Aizoaceae: non-Mesembryanthema), co-dominant with the grass *Stipagrostis sabulicola* in the coastal part of the main dune field and its extension north of Walvis Bay, supports several species of *Quartinia*, which seem to be restricted to it. In recent years we have noted ever increasing destruction of dune vegetation and gravel plains vegetation, including that of drainage channels, resulting from an increase in 4x4 and quad bike tourism in the recreational areas.

In the northern Kaokoveld where the Himba people previously practised nomadic stock farming there is a trend towards more permanent settlements along the roads used by tourists, particularly at and south of the Epupa Falls, an observation confirmed by the proprietor of the camping site. Such areas are seriously denuded of vegetation (Figure 165) and water sources are heavily polluted as we observed when collecting in that area, in consequence floral resources, suitable water sources and nesting sites for pollen wasps, other aculeate wasps and bees in that area are greatly reduced.

Land management for maintaining essential populations of pollen wasps, other aculeate wasps and bees: pollinators and predators

Aspects of agricultural land use seen to be adversely affecting the diversity of pollen wasps together with other solitary aculeate wasps and solitary bees are:

- Excessive stocking rates.
- Heavy selective grazing and browsing.
- Excessive trampling.
- Water pollution by stock.
- Large-scale impoundment of water.
- Canalising of water.
- Extensive replacement of natural vegetation by cultivated pastures.
- Extensive replacement of natural vegetation by crop plants.
- Use of insecticides for crop and grazing protection.
- The spread of invasive alien plant species.

To this can be added, for bees and wasps nesting in woody stems and constructing nests on woody stems:

- Bush cutting.
- Intensive removal of dry wood.

To date, no pollen wasps have been found nesting in these situations.

Management practices for maintaining essential populations of pollen wasps, other aculeate wasps and bees on land used for agriculture or game:

- Care can be taken not to overstock, reducing the danger of excessive trampling and excessive selective grazing and browsing.

- The effects of seasonal selective grazing and browsing can be reduced by moving stock at frequent intervals.
- Nesting areas of ground-nesting pollen wasps, other aculeate wasps and bees can be protected from trampling.
- The needs of pollen wasps, other aculeate wasps and bees can be catered for when designing irrigation systems or stock watering points.
- When creating cultivated pastures, strips of natural vegetation can be left untouched.
- When natural vegetation is replaced by crop plants, strips of natural vegetation can be left untouched.
- If insecticides must be used, their effects on organisms in areas other than those targeted can be taken into consideration and precautions taken against contamination of surrounding areas and water sources.
- Invasion by alien plant species can be controlled.
- Bush cutting can be undertaken in such a way that areas or strips of bush-covered land are retained.
- Removal of dry wood can be restricted.
- Populations of cavity users can be enhanced by the provision of blocks of wood drilled with suitable holes.

When flower reserves or general nature reserves are created, it should be borne in mind that most flowering plants, even those that can self-pollinate in the absence of pollinators, require cross pollination if they are to survive over time. Before delimiting the reserves, preliminary studies of the area should be undertaken to establish what insects are associated with what plants and what the requirements of those insects are. At least in the case of pollen wasps, other aculeate wasps and bees, it should be possible to ensure that their nesting sites are included in the reserve and that requirements such as suitable water sources are supplied.

Coastal development and invasion by alien plants and snails

Coastal development has accelerated alarmingly over the past 10 years. Particularly disturbing has been destruction of dunes and dune vegetation as a 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. Pollen wasps affected by this type of destructive development are principally species of *Quartinia* and *Celonites*.

The destructive effect of the introduction of and spread of Australian acacias is well documented.

Most investigations of the spread of the Mediterranean snail *Theba pisana* (Helicidae) (Figure 166) relate to its impact in the field of agriculture where its effects on production and therefore on monetary returns are of concern. Little attention seems to have been paid to its impact on natural systems. *Theba pisana* was apparently introduced into Cape Town from Europe at around 1881. It has since spread northwards along the west coast at least to Port Nolloth and eastwards along the south coast at least as far as East London. In the west its invasion of vineyards and citrus orchards has been investigated by the Agricultural Research Council. It has been the subject of considerable study





FIGURE 166. *Theba pisana* inland from Port Nolloth.

in South Australia, 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 effects of the spread of *Theba pisana* along the coast. Sand-filled empty shells of terrestrial snails, *Trigonephrus* species on the west and western south coast and *Tropidophora ligata* (Pomatiidae) on the south and southeast coast, living amongst the dunes, are used for nesting by *Quartinia* species and empty shells are used for nesting by cavity-nesting bees and wasps. *Theba pisana* is out-competing these indigenous snails to such an extent that in most areas where they occur they vastly outnumber the indigenous snails. Apart from the obvious threat they pose to indigenous snails, they also have an impact on the populations of snail shell users. They are considerably smaller in volume than the shells of *Trigonephrus* and although not appreciably smaller in volume than those of *T. ligata*, have a flat crown, unlike the relatively tall crown of *T. ligata*. They are therefore unsuited for nesting by larger snail shell users and less suited for nesting by *Quartinia* as they can house far fewer cells, and cells constructed in a flat crown are less secure than those constructed in a taller crown.

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Appendix 1

Variations in familial classification of flowering plant families visited by pollen wasps in southern Africa

Cronquist 1988	A.P.G. 1998	Leistner 2000	Germishuizen & Meyer 2003	Present work	Historical names
Aizoaceae	Aizoaceae	Aizoaceae Mesembryanthemaceae	Aizoaceae Mesembryanthemaceae	Aizoaceae	
Molluginaceae	Molluginaceae	Molluginaceae Gisekiaceae	Molluginaceae Gisekiaceae	Molluginaceae	All formerly included in Aizoaceae
Asteraceae	Asteraceae	Asteraceae	Asteraceae	Asteraceae	Compositae
Scrophulariaceae	Scrophulariaceae	Scrophulariaceae	Scrophulariaceae	Scrophulariaceae	
Campanulaceae	Campanulaceae	Campanulaceae Lobeliaceae	Campanulaceae Lobeliaceae	Campanulaceae	
Zygophyllaceae	Zygophyllaceae	Zygophyllaceae	Zygophyllaceae	Zygophyllaceae	
Mimosaceae Caesalpinaceae Fabaceae	Fabaceae	Fabaceae	Fabaceae	Fabaceae	Leguminosae
Malvaceae Sterculiaceae	Malvaceae	Malvaceae Sterculiaceae	Malvaceae Sterculiaceae	Malvaceae	
Geraniaceae	Geraniaceae	Geraniaceae	Geraniaceae	Geraniaceae	
Boraginaceae Hydrophyllaceae	Boraginaceae	Boraginaceae	Boraginaceae Hydrophyllaceae	Boraginaceae	
Crassulaceae	Crassulaceae	Crassulaceae	Crassulaceae	Crassulaceae	
Neuradaceae	Neuradaceae	Neuradaceae	Neuradaceae	Neuradaceae	
Amaranthaceae	Amaranthaceae	Amaranthaceae	Amaranthaceae	Amaranthaceae	
Acanthaceae	Acanthaceae	Acanthaceae	Acanthaceae	Acanthaceae	
Lamiaceae	Lamiaceae	Lamiaceae	Lamiaceae	Lamiaceae	Labiatae
Nyctaginaceae	Nyctaginaceae	Nyctaginaceae	Nyctaginaceae	Nyctaginaceae	
Plumbaginaceae	Plumbaginaceae	Plumbaginaceae	Plumbaginaceae	Plumbaginaceae	
Euphorbiaceae	Euphorbiaceae	Euphorbiaceae	Euphorbiaceae	Euphorbiaceae	
Brassicaceae Capparaceae	Brassicaceae	Brassicaceae Capparaceae	Brassicaceae Capparaceae	Brassicaceae	Cruciferae
Vahliaceae	Vahliaceae	Vahliaceae	Vahliaceae	Vahliaceae	
Asphodelaceae Aloaceae	Asphodelaceae	Asphodelaceae	Asphodelaceae	Asphodelaceae	Liliaceae
Iridaceae	Iridaceae	Iridaceae	Iridaceae	Iridaceae	Iridaceae

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Appendix 2

Records of flower visiting by pollen wasps in southern Africa

Unless otherwise stated, northern Nama-Karoo refers to South Africa.

Unless otherwise indicated, the records are those of the Gess Family, mostly F.W. and S.K. Gess.

Abbreviations, flower colours: B – blue; G – green; O – orange; Pi – pink; Pu – purple; R – red; V – violet; W – white; Y – yellow.

Plant families visited are listed under each pollen wasp species. Marked preferences are indicated by these families being given only in bold.

Full locality details are available from the voucher specimen labels.

Priscomasarina

Priscomasaris Gess, western Namibia

Priscomasaris namibiensis Gess, western Namibia

Aizoaceae: non-Mesembryanthema, many records and provision

<i>Sesuvium sesuvioides</i> (Fenzl) Verdc.	PuPi	Namibia, southern
<i>Trianthema parvifolia</i> E.Mey. ex Sond.	W	Namibia, southern

Molluginaceae, many records and provision

<i>Gisekia africana</i> (Lour.) Kuntze	Pi	Namibia, southern; Namibia, northwestern
<i>Limeum argute-carinatum</i> Wawra & Peyr.	W	Namibia, northwestern
<i>Limeum myosotis</i> H.Walter	W	Namibia, northwestern
<i>Limeum sulcatum</i> (Klotsch) Hutch.	W	Namibia, northwestern

Euphorbiaceae, extra-floral nectaries only, unusual

<i>Euphorbia glanduligera</i> Pax	–	Namibia, northwestern
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Masarina

Ceramius Latreille, Groups 1 and 7 circum Mediterranean, Groups 2 to 6 and 8 southern Africa

***Ceramius* Group 2a**

Ceramius brevitarsis Gess, Richtersveld, Namaqualand

Zygophyllaceae, few records

<i>Zygophyllum prismatocarpum</i> E.Mey. ex Sond.	YW	Namaqualand, Richtersveld
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Ceramius cerceriformis de Saussure, Namaqualand, southern and Little Karoo

Aizoaceae: Mesembryanthema, solely, many records

<i>Aridaria</i> sp.	W	Olifants River Valley
<i>Mesembryanthemum pallens</i> (Aiton) N.E.Br.	WPi	Olifants River Valley; Namaqualand
'mesemb'	YO	Namaqualand

Ceramius peringueyi Brauns, southern Namaqualand to north of the Olifants River Mountains

Aizoaceae: Mesembryanthema, solely, many records

<i>Prekia pallens</i> (Aiton) N.E.Br.	WPI	west and northwest of the Olifants River Valley
<i>Psilocaulon acutisepalum</i> (A.Berger) N.E.Br.	WPI	Vredendal
<i>Psilocaulon junceum</i> (Haw.) Schwantes	Pi	west of Olifants River Valley

Ceramius Group 2b

***Ceramius clypeatus* Richards, Olifants River Valley and to the west**

Fabaceae: Papilionoideae: Cape Crotalariaeae, solely, many records, provision

<i>Aspalathus linearis</i> (Burm.f.) R.Dahlgren	Y	Olifants River Valley
<i>Aspalathus pulicifolia</i> R.Dahlgren	Y	Olifants River Valley and to the west
<i>Aspalathus spinescens</i> Thunb.	Y	Olifants River Valley and to the west
<i>Aspalathus vulnerans</i> Thunb.	Y	Olifants River Valley

***Ceramius richardsi* Gess, Olifants River Valley and southwestern West Cape**

Fabaceae: Papilionoideae: Cape Crotalariaeae, solely

<i>Aspalathus pulicifolia</i> R.Dahlgren	Y	Olifants River Valley
'legume'	–	Western Cape, southwestern, Philadelphia (Whitehead)

***Ceramius micheneri* Gess, Olifants River Valley**

Fabaceae: Papilionoideae: Cape Crotalariaeae, solely, many records, provision

<i>Aspalathus pulicifolia</i> R.Dahlgren	Y	Olifants River Valley
<i>Aspalathus spinescens</i> Thunb.	Y	Olifants River Valley

Ceramius Group 3

***Ceramius braunsi* Turner, Olifants River Valley and, southeastern Nama-Karoo Willowmore**

Asteraceae, almost solely, many records, provision

<i>Arctotheca calendula</i> (L.) Levyns	Y	Olifants River Valley
<i>Arctotis laevis</i> Thunb.	Y	Olifants River Valley
<i>Athanasia trifurcata</i> (L.) L.	Y	Olifants River Valley
<i>Berkheya fruticosa</i> (L.) Ehrh.	Y	Olifants River Valley
<i>Leysera</i> sp.	Y	Olifants River Valley
<i>Oncosiphon grandiflorum</i> (Thunb.) Källersjö	Y	Olifants River Valley
<i>Pteronia divaricata</i> (P.J.Bergius) Less.	Y	Olifants River Valley

Fabaceae: Papilionoideae: Cape Crotalariaeae, exceptional, for nectar collection

<i>Aspalathus spinescens</i> Thunb.	Y	Olifants River Valley
<i>Lebeckia sericea</i> Thunb.	Y	Olifants River Valley

***Ceramius jacoti* Richards, western Little Karoo**

Asteraceae, solely, many records, provision

<i>Pteronia incana</i> (Burm.) DC.	Y	Little Karoo (Jacot Guillarmod)
<i>Senecio rosmarinifolius</i> L.f.	Y	Little Karoo

***Ceramius nigripennis* de Saussure, Namaqualand**

Asteraceae, solely, many records, provision

<i>Arctotheca calendula</i> (L.) Levyns	Y	Namaqualand
<i>Arctotis laevis</i> Thunb.	Y	Namaqualand
<i>Berkheya fruticosa</i> (L.) Ehrh.	Y	Namaqualand
<i>Berkheya onobromoides</i> (DC.) O.Hoffm. & Muschl.	Y	Namaqualand
<i>Dimorphotheca sinuata</i> DC.	O	Namaqualand
<i>Hirpicium alienatum</i> (Thunb.) Druce	Y	Namaqualand
<i>Leysera gnaphalodes</i> (L.) L.	Y	Namaqualand
<i>Pentzia suffruticosa</i> (L.) Hutch. ex Merxm.	Y	Namaqualand
<i>Pteronia incana</i> (Burm.) DC.	Y	Namaqualand
<i>Senecio</i> cf. <i>cinerascens</i> Aiton	Y	Namaqualand

***Ceramius toriger* von Schulthess, southwestern Namaqualand and Tankwa Karoo**

Asteraceae, solely, many records, provision

<i>Athanasia trifurcata</i> (L.) L.	Y	Tankwa Karoo, Karoo Poort
<i>Berkheya fruticosa</i> (L.) Ehrh.	Y	Namaqualand, southwestern
<i>Pteronia divaricata</i> (P.J.Bergius) Less.	Y	Namaqualand, southwestern
'blue rayed'	B	Tankwa Karoo (Michener)

***Ceramius* Group 4**

***Ceramius beyeri* Brauns, widely distributed in southern South Africa**

Aizoaceae: Mesembryanthema, solely

<i>Prenia pallens</i> (Aiton) N.E.Br	Pi	Olifants River Valley
<i>Phyllobolus</i> cf. <i>splendens</i> (L.) Gerbaulet	WPi	Nama-Karoo, southern
'mesemb'	W	Nama-Karoo, eastern

***Ceramius damarinus* Turner, widely distributed in Namibia from the south, northwards to the Kunene**

Aizoaceae: non-Mesembryanthema, many records, provision

<i>Sesuvium sesuvioides</i> (Fenzl) Verdc.	PuPi	Namibia, southern; Namibia, northwestern to the Kunene River
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Acanthaceae, one male only

'acanth'	–	Namibia, northwestern
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Amaranthaceae, four females

<i>Hermbsaedia odorata</i> (Burch.) T.Cooke	Pi	Namibia, northwestern
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Lamiaceae, four females and eight males

<i>Ocimum americanum</i> L.	V	Namibia, northwestern
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Molluginaceae (ex Aizoaceae: non-Mesembryanthema), males only

<i>Gisekia africana</i> (Lour.) Kuntze	Pi	Namibia, northwestern
<i>Limeum myosotis</i> H.Walter	W	Namibia, northwestern

Scrophulariaceae, one male

<i>Selago dinteri</i> Rolfe	W	Namibia, west of Windhoek
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Zygophyllaceae, one male

<i>Tribulus</i> sp.	Y	Namibia, northwestern
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Ceramius Group 5

***Ceramius lichtensteinii* Klug, widely distributed in southern South Africa east of the western escarpment**

Acanthaceae, occasional, casual for nectar only

<i>Blepharis capensis</i> (L.f.) Pers.	W	Nama-Karoo, southeastern
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Aizoaceae: Mesembryanthema, many records, provision

<i>Aridaria</i> sp.	WY	Nama-Karoo, southeastern
<i>Mesembryanthemum aitonis</i> Jacq.	W	Nama-Karoo, southeastern
<i>Ruschia</i> sp.	W	Nama-Karoo, southeastern
<i>Ruschia</i> sp.	PuPi	Nama-Karoo, southeastern
<i>Phyllobolus</i> cf. <i>splendens</i> (L.) Gerbaulet	WPi	Nama-Karoo, southern

Asteraceae, occasional, casual, when no mesembs in flower

<i>Pteronia</i> sp.	Y	Nama-Karoo, southern
<i>Senecio pterophorus</i> DC.	Y	Nama-Karoo, southeastern

Ceramius Group 6

***Ceramius caffer* de Saussure, southwestern Western Cape, south of the Olifants River Mountains, and one site east of the Cederberg**

Asteraceae, solely, few records

<i>Berkheya carlinifolia</i> (DC.) Roessler	Y	Western Cape, southern
<i>Berkheya</i> sp.	Y	Western Cape, southern (Whitehead)

***Ceramius metanotalis* Richards, Olifants River Valley and Cederberg**

Asteraceae, solely, many records, provision

<i>Athanasia trifurcata</i> (L.) L.	Y	Olifants River Valley
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***Ceramius rex* de Saussure, Namaqualand Klipkoppe**

Asteraceae, solely, provision

<i>Berkheya canescens</i> DC.	Y	Namaqualand
<i>Berkheya onobromoides</i> (DC.) O.Hoffm. & Muschl.	Y	Namaqualand
<i>Pteronia</i> sp.	Y	Namaqualand

Ceramius Group 8

***Ceramius bicolor* (Thunberg), widespread in southwestern South Africa**

Aizoaceae: Mesembryanthema, many records, provision

<i>Drosanthemum</i> sp.	Pi	Namaqualand, southwestern
<i>Prenia pallens</i> (Aiton) N.E.Br.	WPi	Olifants River Valley; Namaqualand
<i>Psilocaulon</i> cf. <i>utile</i> L.Bolus	Pi	Tankwa Karoo, Karoo Poort

***Ceramius capicola* Brauns, southeastern South Africa and Free State**

Aizoaceae: Mesembryanthema, many records, provision

<i>Aridaria dyeri</i> L.Bolus	YW	Nama-Karoo, southeastern
<i>Aridaria plenifolia</i> (N.E.Br.) Stearn	YW	Nama-Karoo, southeastern
<i>Drosanthemum floribundum</i> (Haw.) Schwantes	Pi	Nama-Karoo, southeastern
<i>Mesembryanthemum aitonis</i> Jacq.	W	Nama-Karoo, southeastern
<i>Mestoklema tuberosum</i> (L.) N.E.Br.	PuPi	Nama-Karoo, southeastern
<i>Platythra haeckeliana</i> (A.Berger) N.E.Br.	Y	Nama-Karoo, southeastern
<i>Ruschia</i> sp.	PuPi	Nama-Karoo, southeastern
<i>Ruschia</i> sp.	W	Nama-Karoo, southeastern

Asteraceae, one female, one male

<i>Berkheya</i> sp.	Y	Free State (Jacot Guillarmod)
<i>Pentzia incana</i> (Thunb.) Kuntze	Y	Free State, eastern

***Ceramius linearis* Klug, widespread southern South Africa**

Aizoaceae: Mesembryanthema, solely, many records, provision

<i>Aridaria dyeri</i> L.Bolus	YW	Nama-Karoo, southeastern
<i>Aridaria plenifolia</i> (N.E.Br.) Stearn	YW	Nama-Karoo, southeastern
<i>Drosanthemum floribundum</i> (Haw.) Schwantes	Pi	Nama-Karoo, southeastern
<i>Malephora</i> sp.	YW	Nama-Karoo, southeastern
<i>Mesembryanthemum aitonis</i> Jacq.	W	Nama-Karoo, southeastern
<i>Psilocaulon</i> cf. <i>absimile</i> N.E.Br.	YW	Nama-Karoo, southeastern
<i>Ruschia</i> sp.	PuPi	Nama-Karoo, southeastern
<i>Ruschia</i> sp.	W	Nama-Karoo, southeastern

***Ceramius socius* Turner, southwestern Western Cape**

Aizoaceae: Mesembryanthema, many records, provision

<i>Prenia pallens</i> (Aiton) N.E.Br.	WPi	Olifants River Valley
<i>Psilocaulon junceum</i> (Haw.) Schwantes	Pi	west of Olifants River Valley
'mesemb'	Pi	Little Karoo, western
'mesemb'	W	Touws River

Campanulaceae, one male

<i>Wahlenbergia paniculata</i> (Thunb.) A.DC.	V	Olifants River Valley
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Jugurtia* de Saussure, circum-Mediterranean and Afrotropical, mainly southern Africa**Jugurtia alkfeni* (du Buysson), widespread in Namibia, Botswana and southern South Africa****Malvaceae (Sterculiaceae), many records**

<i>Hermannia modesta</i> (Ehrenb.) Mast.	Pi to R	Namibia, southern; Namibia, southeastern Nama-Karoo; Namibia, southern Kalahari; Namibia, western central, west of Windhoek; Namibia, northwestern; Namibia, northern; Namibia, Kaokoveld
<i>Hermannia spinosa</i> E.Mey. ex Harv.	R	Namibia, northwestern
<i>Hermannia linearifolia</i> Harv.	R	southeastern Nama-Karoo

Asteraceae, one male

<i>Pentzia incana</i> (Thunb.) Kuntze	Y	Namibia, west of Windhoek
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Brassicaceae (Capparaceae), one male

<i>Cleome elegantissima</i> Briq.	PiV	Namibia, northwestern
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Combretaceae, one female

<i>Terminalia prunioides</i> M.A.Lawson	W	Namibia, northwestern
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Lamiaceae, one female

<i>Ocimum americanum</i> L.	V	Namibia, northwestern
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Jugurtia braunsi* (von Schulthess), widespread in southwestern South Africa*Aizoaceae: Mesembryanthema, many records**

<i>Conicosia</i> sp.	Y	west of Olifants River Valley
<i>Drosanthemum hispidum</i> (L.) Schwantes	Pi	Namaqualand, Klipkoppe
<i>Drosanthemum</i> sp.	Pi	Namaqualand, southeastern
<i>Drosanthemum</i> sp.	Pi	Namaqualand, Knersvlakte
<i>Herrea</i> sp.	Y	Namaqualand, Klipkoppe
<i>Herrea</i> sp.	Y	Namaqualand, southeastern
<i>Leipoldtia constricta</i> (L.Bolus) L.Bolus	Pi	Namaqualand, Klipkoppe
<i>Ruschia</i> sp.	Pi	Namaqualand, Klipkoppe

Aizoaceae: non-Mesembryanthema, four females

<i>Galenia sarcophylla</i> Fenzl	Pi	Namaqualand, Klipkoppe
<i>Tetragonia</i> sp.		Namaqualand, Klipkoppe

Asphodelaceae

<i>Trachyandra muricata</i> (L.f.) Kunth		Olifants River Valley
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Asteraceae, widespread but fewer records than Mesembryanthema

<i>Arctotheca calendula</i> (L.) Levyns	Y	Namaqualand, Klipkoppe
<i>Leysera gnaphalodes</i> (L.) L.	Y	Namaqualand, Klipkoppe
<i>Pentzia suffruticosa</i> (L.) Hutch. ex Merxm.	Y	Namaqualand, southeastern
<i>Pteronia divaricata</i> (P.J.Bergius) Less.	Y	Namaqualand, southeastern; Olifants River Valley
<i>Pteronia incana</i> (Burm.) DC.	Y	Robertson Karoo
<i>Senecio</i> sp.	Y	Namaqualand, Klipkoppe

<i>Senecio</i> sp.	Y	Namaqualand, southeastern
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Campanulaceae, few records

<i>Wahlenbergia pilosa</i> H.Buek	V	Namaqualand, Klipkoppe
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Scrophulariaceae, few records

<i>Polycarena cephalophora</i> (Thunb.) Levyns	W	Namaqualand, Klipkoppe
<i>Selago minutissima</i> Choisy	W	Namaqualand, Klipkoppe
<i>Selago verna</i> Hilliard	W	Namaqualand, Klipkoppe

***Jugurtia braunsiella* (von Schulthess), widespread in southwestern South Africa**

Asteraceae, solely, widespread records, provision

<i>Athanasia trifurcata</i> (L.) L.	Y	Olifants River Valley
<i>Felicia</i> sp.	B	Namaqualand, Klipkoppe
<i>Lasiospermum bipinnata</i> (Thunb.) Druce	W	southeastern Nama-Karoo
<i>Pteronia</i> cf. <i>divaricata</i> (P.J.Bergius) Less.	Y	Namaqualand
<i>Pentzia incana</i> (Burm.) DC.	Y	Namaqualand, southeastern
<i>Senecio burchellii</i> DC.	Y	Karoo Poort , Tankwa Karoo
<i>Senecio rosmarinifolius</i> L.f.	Y	Karoo Poort , Tankwa Karoo, Little Karoo
'composite'	Y	Robertson Karoo

***Jugurtia calcarata* Richards, widespread but uncommon in southwestern South Africa**

Aizoaceae: Mesembryanthema, three females

<i>Drosanthemum</i> sp.	Pi	Namaqualand, southeastern
<i>Prenia pallens</i> (Aiton) N.E.Br.	WPi	Namaqualand, Klipkoppe; west of Olifants River Valley

Asteraceae, one female

<i>Pentzia suffruticosa</i> (L.) Hutch. ex Merxm.	Y	Namaqualand, southeastern
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***Jugurtia codoni* Gess, Richtersveld, Namaqualand**

Boraginaceae (Hydrophyllaceae), many records, nectar and pollen

<i>Codon royenii</i> L.	W	Namaqualand, Richtersveld
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Amaranthaceae, three females

<i>Hermstaedtia glauca</i> (J.C.Wendl.) Rchb. ex Steud.	Pi	Namaqualand, Richtersveld
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Asteraceae, three females

<i>Senecio arenarius</i> Thunb.	PuPi	Namaqualand, Richtersveld
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Geraniaceae, nine females, one male

<i>Pelargonium klinghardtense</i> Kunth	W	Namaqualand, Richtersveld
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Scrophulariaceae, eight females

<i>Peliospermum</i> sp.	PV	Namaqualand, Richtersveld
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Zygophyllaceae, two females

<i>Zygophyllum prismatocarpum</i> E.Mey. ex Sond.	W	Namaqualand, Richtersveld
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<i>Zygophyllum foetidum</i> Schrad. & J.C.Wendl. (= <i>Z. meyeri</i> Sond.)	Y	Namaqualand, Richtersveld
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***Jugurtia confusa* Richards, widespread in South Africa, Namibia west of Windhoek**

Aizoaceae: Mesembryanthema, few BUT also provision

<i>Drosanthemum parvifolium</i> (Haw.) Schwantes	Pi	Namaqualand, southeastern
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Malvaceae (Sterculiaceae), many records, one day, one site

<i>Hermannia comosa</i> Burch. ex DC.	Y	Namibia west of Windhoek
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Fabaceae: Mimosoideae, casual, one female

<i>Acacia karroo</i> Hayne	Y	Nama-Karoo, southeastern
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***Jugurtia damara* Gess, extreme south of Angola and northern Namibia**

Malvaceae (Sterculiaceae), solely

<i>Hermannia modesta</i> (Ehrenb.) Mast.	Pi to R	Namibia, southern; Namibia, western central; Namibia, northwestern
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***Jugurtia discrepans* Brauns, widely scattered from the extreme southwest of Namibia through the karroid areas of South Africa**

Asteraceae, two females

<i>Senecio burchellii</i> DC.	Y	Karoo Poort, Tankwa Karoo
<i>Senecio rosmarinifolius</i> L.f.	Y	Karoo Poort, Tankwa Karoo

***Jugurtia duplicata* Richards, Klipkoppe, Namaqualand**

No flower-visiting records.

***Jugurtia eburnea* (Turner), widely scattered in the karroid areas of South Africa**

Asteraceae, solely

<i>Leysera gnaphalodes</i> (L.) L.	Y	Namaqualand, southeastern
<i>Osteospermum oppositifolium</i> (Aiton) Norl.	Y	Namaqualand, southeastern
<i>Senecio</i> prob. <i>niveus</i> (Thunb.) Willd.	W	Namaqualand, southeastern

***Jugurtia einensis* Gess, Richtersveld and Klipkoppe, Namaqualand, and its northeastern fringe**

No flower-visiting records.

***Jugurtia elegans* Gess, northern, northwestern Namibia**

Asteraceae, one female

<i>Ondetia linearis</i> Benth.	Y	Namibia, northwestern
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***Jugurtia gariepensis* Gess, Richtersveld, Namaqualand, and northwestern Bushmanland**

No flower-visiting records.

***Jugurtia hessei* Gess**

No flower-visiting records.

***Jugurtia koeroegabensis* Gess**

Asteraceae, three females

<i>Osteospermum</i> sp.	Y	Namaqualand, Richtersveld
<i>Pteronia</i> sp.	Y	Namibia, Sperrgebiet

Brassicaceae (Capparaceae), one female

<i>Cleome paxii</i> (Schinz) Gilg & Ben.	Y	Namaqualand, Richtersveld
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Iridaceae, two females

<i>Ferraria variabilis</i> Goldblatt & J.C.Manning	GY	Namaqualand, Richtersveld
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Scrophulariaceae, six females, 15 males

<i>Peliostomum leucorrhizum</i> E.Mey. ex Benth.	BV	Namaqualand, Richtersveld
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Zygophyllaceae, three females

<i>Zygophyllum prismatocarpum</i> E.Mey. ex Sond.	YW	Namaqualand, Richtersveld
<i>Zygophyllum foetidum</i> Schrad. & J.C.Wendl. (= <i>Z. meyeri</i> Sond.)	Y	Namaqualand, Richtersveld

Jugurtia mandibulata* Gess*Malvaceae (Sterculiaceae), principally**

<i>Hermannia modesta</i> (Ehrenb.) Mast.	Pi – R	Namibia, southern; Namibia, south-eastern; Namibia, west of Windhoek; Namibia northwestern
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Molluginaceae, one female

<i>Gisekia africana</i> (Lour.) Kuntze	Pi	Namibia, northwestern
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Jugurtia namibicola* Gess*Boraginaceae, many records**

<i>Heliotropium tubulosum</i> E.Mey. ex DC.	W	Namibia, northwestern
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Jugurtia nigrifrons* Gess, western karroid areas of South Africa*Aizoaceae: Mesembryanthema, small samples but numerous localities**

<i>Drosanthemum hispidum</i> (L.) Schwantes	Pi	Namaqualand, Klipkoppe
<i>Drosanthemum</i> sp.	Pi	Namaqualand, Knersvlakte
<i>Drosanthemum</i> sp.	Pi	Namaqualand, Richtersveld
<i>Leipoldtia constricta</i> (L.Bolus) L.Bolus	Pi	Namaqualand, Klipkoppe
'cone flower'	W	Namaqualand, southeastern
'mesemb'	Pi	Namaqualand, southeastern
'mesemb'	PuPi	Namaqualand, southeastern

Asteraceae, two females

<i>Pteronia</i> cf. <i>divaricata</i> (P.J.Bergius) Less.	Y	Namaqualand, southeastern
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***Jugurtia saussurei* (Brauns), Namaqualand, Olifants River Valley and eastwards, Little Karoo**

No flower-visiting records. (since going to press *J. saussurei* females have been collected from flowers of Aizoaceae: Mesembryanthema and Asteraceae in the central Karoo and of Campanulaceae and Scrophulariaceae, Selaginaceae in the western Karoo).

***Jugurtia spinolae* (de Saussure), two females, no locality**

No flower-visiting records.

Jugurtia tibialis* Gess, western Namibia*Asteraceae, only**

<i>Geigeria pectidea</i> (DC.) Harv.	Y	Namibia, southwestern; Namibia, north-western
<i>Ondetia ornativa</i> O.Hoffm.	Y	Namibia, northwestern

***Jugurtia tigrina* Gess, Namaqualand, Tankwa Karoo, southern Karoo**

Asteraceae, two females, one male

<i>Leysera gnaphalodes</i> (L.) L.	Y	Namaqualand, southeastern
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Jugurtia turneri* Gess, southern Tankwa Karoo*Asteraceae, solely**

<i>Athanasia trifurcata</i> (L.) L.	Y	Karooport, Tankwa Karoo
<i>Athanasia</i> sp.	Y	Karooport, Tankwa Karoo
<i>Senecio rosmarinifolius</i> L.f.	Y	Karooport, Tankwa Karoo

***Jugurtia zebra* Gess, Little Karoo**

No flower-visiting records.

Masarina* Richards, a southern African endemic**Masarina aptosimi* Gess****Scrophulariaceae, solely**

<i>Aptosimum albomarginatum</i> Marloth & Engl.	Pu	Groblershoop, Nama-Karoo
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Masarina ceres* Gess*Fabaceae: Papilionoideae, solely**

<i>Aspalathus divaricata</i> Thunb.	Y	Gydo Pass, Western Cape
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Masarina familiaris* Richards*Fabaceae: Papilionoideae, solely, many records**

<i>Aspalathus divaricata</i> Thunb.	Y	Gydo Pass, Western Cape
<i>Aspalathus linearis</i> (Burm.f.) R.Dahlgren	Y	Namaqualand, southeastern; Olifants River Valley; west of Olifants River Valley
<i>Aspalathus pulicifolia</i> R.Dahlgren	Y	Olifants River Valley
<i>Aspalathus spinescens</i> Thunb.	Y	Olifants River Valley; west of Olifants River Valley
<i>Lebeckia sericea</i> Thunb.	Y	Namaqualand, Klipkoppe; Olifants River Valley

Masarina hermanniae* Gess*Malvaceae: Sterculioideae, solely**

<i>Hermannia</i> sp.	O	Bushmanland, Aggeneys
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Masarina hyalinipennis Richards**Fabaceae: Papilionoideae, solely, many records**

<i>Aspalathus spinescens</i> Thunb.	Y	west of Olifants River Valley; Namaqualand, Klipkoppe
<i>Melolobium candicans</i> (E.Mey.) Eckl. & Zeyh.	Y	Namaqualand, Klipkoppe
<i>Wiborgia monoptera</i> Thunb.	YW	Namaqualand, Klipkoppe

Masarina mixta Richards

Asteraceae, one record

<i>Athanasia trifurcata</i> (L.) L.	Y	Olifants River Valley
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Campanulaceae, mostly

<i>Wahlenbergia annularis</i> A.DC.	V	Olifants River Valley
<i>Wahlenbergia paniculata</i> (Thunb.) A.DC.	V	Olifants River Valley
<i>Wahlenbergia psammophila</i> Schltr.	V	west of Olifants River Valley
<i>Wahlenbergia</i> sp.	V	Namaqualand, Klipkoppe

Fabaceae: Papilionoideae, one record

<i>Aspalathus spinescens</i> Thunb.	Y	Olifants River Valley
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Malvaceae: Sterculioideae, one record

<i>Hermannia (Mahernia)</i> sp.	PiO	Olifants River Valley
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Scrophulariaceae, two records

<i>Peliostomum</i> sp.	PV	Namaqualand, Richtersveld
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Masarina mixtoides Gess

Asteraceae, one record

'composite'	Y	Namaqualand, Richtersveld
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Campanulaceae, one record

<i>Wahlenbergia</i> sp.	V	Olifants River Valley
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Geraniaceae, mostly

<i>Pelargonium klinghardtense</i> Knuth	W	Namaqualand, Richtersveld
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Zygophyllaceae, few

<i>Zygophyllum foetidum</i> Schrad. & J.C.Wendl. (= <i>Z. meyeri</i> Sond.)	Y	Namaqualand, Richtersveld
<i>Zygophyllum prismatocarpum</i> E.Mey. ex Sond.	YW	Namaqualand, Richtersveld

Masarina namaqua Gess

Campanulaceae, two records

<i>Wahlenbergia</i> cf. <i>prostrata</i> A.DC.	V	Namaqualand, Klipkoppe
<i>Wahlenbergia oxyphylla</i> A.DC.	V	Namaqualand, Klipkoppe



Masarina parvula Gess**Campanulaceae, solely**

<i>Wahlenbergia oxyphylla</i> A.DC.	V	Namaqualand, Klipkoppe
<i>Wahlenbergia</i> sp.	V	Namaqualand, Klipkoppe

Masarina peliostomi Gess**Scrophulariaceae, solely**

<i>Peliostomum</i> sp.	PuV	Namaqualand, Richtersveld
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Masarina roberti Gess

Asteraceae, one record

<i>Osteospermum</i> sp.	Y	Namibia, 'Richtersveld'
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Masarina strucki Gess**Malvaceae: Sterculioideae, solely, many records and provision**

<i>Hermannia disermifolia</i> Jacq.	Y	Namaqualand, Klipkoppe
<i>Hermannia vestita</i> Thunb.	Y	Little Karoo, western
<i>Hermannia</i> sp.	PiO	Olifants River Valley

Masarina tylecodoni Gess**Crassulaceae, solely, many records**

<i>Tylecodon hallii</i> (Tölken) Tölken	Y	Namaqualand, Richtersveld
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Celonites Latreille, Palaearctic, mainly circum Mediterranean and Afrotropical, mainly southern Africa

Celonites andrei Brauns**Scrophulariaceae, mainly**

<i>Aptosimum procumbens</i> (Lehm.) Steud.	BV	Nama-Karoo, southeastern
<i>Aptosimum spinescens</i> (Thunb.) Weber	PuV	Namaqualand, Klipkoppe; Kalahari, south
<i>Peliostomum virgatum</i> E.Mey. ex Benth.	PuV	Namaqualand, Klipkoppe

Campanulaceae, two specimens

<i>Lobelia anceps</i> L.f.	WV	Nama-Karoo, eastern
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Celonites arenarius Gess, known only from Pachtvlei, on the southern bank of the Orange River, 7 km from its mouth

No flower-visiting records.

Celonites bergenwaliae Gess

Aizoaceae: Mesembryanthema, few

<i>Conicosia</i> sp.	Y	west of Olifants River Valley
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Asteraceae, few

<i>Senecio</i> cf. <i>arenarius</i> Thunb.	Pi	west of Olifants River Valley
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Campanulaceae, mostly

<i>Wahlenbergia</i> cf. <i>constricta</i> Brehmer	BV	west of Olifants River Valley
<i>Wahlenbergia psammophila</i> Schltr.	PuV	west of Olifants River Valley

Geraniaceae, one record

<i>Pelargonium capitatum</i> (L.) L'Hér.	Pi	west of Olifants River Valley
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***Celonites capensis* Brauns**

Aizoaceae: Mesembryanthema, two records, one site

<i>Prekia pallens</i> N.E.Br.	WPI	Namaqualand, Klipkoppe
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Asteraceae, many records

<i>Berkheya heterophylla</i> (Thunb.) O.Hoffm.	Y	Nama-Karoo, southeastern
<i>Berkheya</i> sp.	Y	Nama-Karoo, southeastern; Little Karoo
<i>Osteospermum</i> sp.	Y	Namibia, 'Richtersveld'
<i>Senecio pterophorus</i> DC.	Y	Nama-Karoo, southeastern

Boraginaceae, one male

<i>Ehretia rigida</i> (Thunb.) Druce	PiV	Nama-Karoo, southeastern
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Campanulaceae, two males

<i>Wahlenbergia ecklonii</i> H.Buek	V	Gydo Pass, Western Cape
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Geraniaceae, many records

<i>Pelargonium myrrhifolium</i> (L.) L'Hér.	WR	Little Karoo
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Iridaceae, two females

<i>Ferraria kamiesbergensis</i> M.P.de Vos	GY	Namaqualand, Klipkoppe
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Scrophulariaceae, few

<i>Phyllopodium cuneifolium</i> (L.f.) Benth.	BV	Nama-Karoo, southeastern
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Celonites clypeatus* Brauns*Scrophulariaceae, solely, many records, many sites**

<i>Aptosimum indivisum</i> Burch.	BV	Namaqualand, Klipkoppe
<i>Aptosimum procumbens</i> (Lehm.) Steud.	BV	Nama-Karoo, southeastern
<i>Aptosimum spinescens</i> (Thunb.) Weber	PuV	Kalahari, southern; Namibia; Nama-Karoo, southern
<i>Peliostomum virgatum</i> E.Mey. ex Benth.	PuV	Namaqualand, Klipkoppe
<i>Peliostomum</i> sp.		Namaqualand, Richtersveld

***Celonites davidi* Gess, southern Richtersveld**

No flower-visiting records.

***Celonites humeralis* Richards, seven females, western Northern Cape**

No flower-visiting records.

Celonites heliotropii* Gess, northwestern Namibia, desert and desert fringe*Boraginaceae, solely, very many**

<i>Heliotropium tubulosum</i> E.Mey. ex DC.	W	Namibia, northern desert fringe
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Celonites kalahariensis* Gess, Kalahari fringe, southeastern Namibia and northern Northern Cape*Scrophulariaceae: Aptosimeae, solely, many**

<i>Aptosimum procumbens</i> (Lehm.) Steud.	BV	Namibia, Kalahari fringe
<i>Aptosimum procumbens</i> (Lehm.) Steud.	BV	Northern Cape, Kalahari fringe

***Celonites latitarsis* Gess, west of the Olifants River Valley**

Aizoaceae: Mesembryanthema, one female, one male

<i>Apatesia</i> sp.	Y	west of Olifants River Valley
<i>Conicosia</i> sp.	Y	west of Olifants River Valley

Campanulaceae, many

<i>Wahlenbergia psammophila</i> Schltr.	Pu	west of Olifants River Valley
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Celonites lobeliae* Gess, southeastern Namaqualand*Campanulaceae, Lobelioideae, solely, one female, one male**

<i>Lobelia linearis</i> Thunb.	Pu	Namaqualand, southeastern
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***Celonites michaelsoni* von Schulthess**

Nyctaginaceae, two males

<i>Boerhavia deserticola</i> Codd	W	Namibia, northeastern desert margin
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Scrophulariaceae, many records, many sites

<i>Anticharis ebracteata</i> Schinz	PuV	Namibia, northern desert
<i>Anticharis inflata</i> Marloth & Engl.	PuV	Namibia, northeastern desert margin
<i>Aptosimum angustifolium</i> Weber & Schinz	PuV	Namibia, northern Nama-Karoo
<i>Aptosimum arenarium</i> Engl.	PV	Namibia, northwestern arid savanna
<i>Aptosimum lineare</i> Marloth & Engl.	PuV	Namibia, northern desert
<i>Aptosimum spinescens</i> (Thunb.) Weber	PuV	Namaqualand, Richtersveld; Namibia; southern Nama-Karoo
<i>Aptosimum</i> sp.	PuV	eastern margin desert, northern Namibia
<i>Peliostomum</i> sp.	PuV	Namaqualand, Richtersveld

Celonites peliostomi* Gess, Namaqualand*Scrophulariaceae, very many**

<i>Aptosimum lineare</i> Marloth & Engl.	BV	Namaqualand, Klipkoppe
<i>Aptosimum indivisum</i> Burch.	BV	Namaqualand, Klipkoppe
<i>Aptosimum spinescens</i> (Thunb.) Weber	PuV	Namaqualand, Klipkoppe; Namaqualand, Richtersveld
<i>Peliostomum virgatum</i> E.Mey. ex Benth.	PuV	Namaqualand, Klipkoppe; Namaqualand, Richtersveld; Namaqualand, southeastern
<i>Peliostomum</i> sp.	PV	Namaqualand, Richtersveld

Celonites promontorii* Brauns, karroid areas of South Africa*Asteraceae, mostly**

<i>Berkheya fruticosa</i> (L.) Ehrh.	Y	Namaqualand, southeast
<i>Berkheya</i> cf. <i>spinosa</i> (L.f.) Druce	Y	Nama-Karoo, southern
<i>Berkheya</i> sp.	not given	Free State, eastern
<i>Pteronia divaricata</i> (P.J.Bergius) Less.	Y	Namaqualand, southeastern
<i>Senecio rosmarinifolius</i> L.f.	Y	Little Karoo (Jacot Guillarmod)

Geraniaceae, one female

<i>Pelargonium klinghardtense</i> Knuth	W	Namaqualand, Richtersveld
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Plumbaginaceae, two females

<i>Limonium</i> sp.	V	Tankwa Karoo, southern
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Celonites pulcher* Gess, northwestern Namibia and western southern Namibia*Scrophulariaceae, Aptosimeae, solely, eight females, two males**

<i>Anticharis scoparia</i> (E.Mey. ex Benth.) Hiern ex Benth. & Hook.f.	Pu	Namibia, southwestern Nama-Karoo
<i>Anticharis inflata</i> Marloth & Engl.	Pu	Namibia, northwestern 'Nama-Karoo'

***Celonites purcelli* Brauns, three females and three males, Eastern Cape**

No flower-visiting records.

Celonites tumidiscutellatus* Gess, Namaqualand, Klipkoppe and Richtersveld*Scrophulariaceae, solely**

<i>Aptosimum indivisum</i> Burch.	BV	Namaqualand, Klipkoppe
<i>Aptosimum spinescens</i> (Thunb.) Weber	PuV	Namaqualand, Richtersveld
<i>Peliostomum leucorrhizum</i> E.Mey. ex Benth.	BV	Namaqualand, Richtersveld

***Celonites turneri* Richards, eastern Northern Cape, described from one male**

No flower-visiting records.

***Celonites wahlenbergiae* Gess, Olifants River Valley and west of Olifants River Valley**

Aizoaceae: Mesembryanthema, secondary

<i>Conicosia</i> sp.	Y	west of Olifants River Valley
<i>Prenia pallens</i> (Aiton) N.E.Br.	Pi	west of Olifants River Valley
<i>Psilocaulon junceum</i> (Haw.) Schwantes	Pi	west of Olifants River Valley

Asteraceae, secondary

<i>Helichrysum</i> sp.	Y	west of Olifants River Valley
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Campanulaceae, mostly

<i>Microcodon sparsiflorum</i> A.DC.	V	west of Olifants River Valley
<i>Wahlenbergia paniculata</i> (Thunb.) A.DC.	BV	Olifants River Valley
<i>Wahlenbergia psammophila</i> Schltr.	PuV	west of Olifants River Valley

Crassulaceae, two females

<i>Crassula dichotoma</i> L.	YO	Olifants River Valley
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Geraniaceae

<i>Pelargonium capitatum</i> (L.) L'Hér.	Pi	west of Olifants River Valley
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Molluginaceae, two females, two males

<i>Coelanthum grandiflorum</i> E.Mey. ex Fenzl	W	west of Olifants River Valley
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Scrophulariaceae

<i>Polycarena cephalophora</i> (Thunb.) Levyns	W	west of Olifants River Valley; Namaqualand, sandveld
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***Celonites wheeleri* Brauns**

Asteraceae, two females

<i>Berkheya</i> cf. <i>spinosa</i> (L.f.) Druce	Y	Nama-Karoo, southern
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Quartinia* Ed. André**Quartinia albopicta* (Richards), Namibia****Aizoaceae: non-Mesembryanthema, solely, very many**

<i>Trianthema hereroensis</i> Schinz	W	Namibia, northern extension of dune desert between Walvis Bay and Swakopmund
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***Quartinia andromeda* (Richards), described from seven females, Western Cape**

No flower-visiting records.

***Quartinia antennata* Richards, described from one female, Western Cape**

No flower-visiting records.

Quartinia antigone* (Richards), Western Cape*Asphodelaceae, solely, many**

<i>Aloe striata</i> Haw.	PiO	Nama-Karoo, southern
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***Quartinia arsinoe* (Richards), described from 43 females, Western Cape and Namibia**

No flower-visiting records.

***Quartinia artemis* Richards, Northern Cape**

Asteraceae, one female

<i>Leysera tenella</i> DC.	Y	Namaqualand, southeastern
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***Quartinia atra* von Schulthess, Western Cape**

Aizoaceae: Mesembryanthema, number of records not given

'Mesembryanthemum'	not given	Montagu (Turner)
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***Quartinia australis* Gess, described from seven females and five males, Western Cape, nesting in snail shells**

No flower-visiting records.

***Quartinia basuto* (Richards), Lesotho**

Asteraceae, one female

<i>Felicia muricata</i> (Thunb.) Nees	BV	Lesotho, western (Jacot Guillarmod)
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***Quartinia breyeri* Richards, described from six females, two males, Zoutpansberg**

No flower-visiting records.

Quartinia bonaespei* Gess, Western Cape, nesting in snail shells*Aizoaceae: Mesembryanthema, eight females**

<i>Conicosia</i> sp.	Y	Western Cape, west coast
<i>Drosanthemum</i> sp.	Pi	Western Cape, west coast
'mesemb'	PuPi	Western Cape, west coast

Asphodelaceae, 14 females

<i>Trachyandra divaricata</i> (Jacq.) Kunth.	W	Western Cape, west coast
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***Quartinia capensis* (Kohl), Western Cape and Eastern Cape**

Aizoaceae: Mesembryanthema, number of records not given

'Mesembryanthemum'	W	Western Cape, southwestern (Turner)
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***Quartinia ceres* (Richards), described from 20 females and three males, Western Cape, Eastern Cape and Northern Cape**

No flower-visiting records.

***Quartinia conchicola* Gess, Western Cape and Northern Cape, nesting in snail shells**

Aizoaceae: Mesembryanthema, four females

<i>Conicosia</i> sp.	Y	Northern Cape, west coast
<i>Drosanthemum</i> sp.	Pi	Northern Cape, west coast

Geraniaceae, one female

<i>Pelargonium klinghardtense</i> Knuth	W	Namaqualand, Richtersveld
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***Quartinia cressida* (Richards), described from 17 females and one male, Western Cape, Northern Cape and Namibia**

No flower-visiting records.

Quartinia cylene* (Richards), Western Cape and Northern Cape*Asteraceae, solely, many**

<i>Athanasia</i> sp.	Y	southern Tankwa Karoo
<i>Leysera gnaphalodes</i> (L.) L.	Y	Namaqualand, Klipkoppe; Namaqualand, southeast
<i>Relhania pumila</i> Thunb.	Y	Namaqualand, southeast
<i>Senecio</i> cf. <i>niveus</i> (Thunb.) Willd.	W	Namaqualand, southeast

***Quartinia cynara* (Richards), described from 10 females, Western Cape and Eastern Cape**

No flower-visiting records.

***Quartinia diana* (Richards), Richtersveld Namaqualand northwards to Aus**

Aizoaceae: Mesembryanthema, two females, three males

<i>Drosanthemum</i> sp.	Pi	Namaqualand, Richtersveld
<i>Psilocaulon</i> sp.	W	Namaqualand, Richtersveld
'mesemb'	Y	Namaqualand, Richtersveld

Asteraceae, one female, two males

'Felicia'	B	Namaqualand, Richtersveld
<i>Gorteria</i> sp.	Y	Namaqualand, Richtersveld

Boraginaceae (Hydrophyllaceae), one female

<i>Codon royenii</i> L.	W	Namaqualand, Richtersveld
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Scrophulariaceae: Aptosimeae, seven females, seven males

<i>Peliostomum leucorrhizum</i> E.Mey. ex Benth.	V	Namaqualand, Richtersveld
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***Quartinia dryope* (Richards), described from one male, Eastern Cape**

No flower-visiting records.

***Quartinia elissa* (Richards), described from 41 females and seven males, Western Cape**

No flower-visiting records.

***Quartinia eurydice* (Richards), described from one female, Northern Cape**

No flower-visiting records.

***Quartinia femorata* Gess, seaward side of dunes, northern extremity of southern Namib, between Walvis Bay and Swakopmund**

Aizoaceae: non-Mesembryanthema, solely, many

<i>Trianthema hereroensis</i> Schinz	W	Namibia, northern extension of dune desert between Walvis Bay and Swakopmund
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***Quartinia flava* (Richards), Northern Cape and Namibia**

Aizoaceae: non-Mesembryanthema, many

<i>Galenia</i> sp.	Pi	Namaqualand, Richtersveld
<i>Galenia</i> sp.	W	Namibia, northern coast
<i>Trianthema parvifolia</i> E.Mey. ex Sond.	Pi	Namibia, southern

Asteraceae, many

'cotula'	Y	Namibia, 'Richtersveld'
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***Quartinia galataea* (Richards), described from one female, Western Cape**

No flower-visiting records.

***Quartinia geigeriae* Gess, Northern Cape and Namibia**

Asteraceae, solely, many

<i>Geigeria ornativa</i> O.Hoffm.	Y	Namibia, northern desert fringe; Namibia southern Nama-Karoo
<i>Geigeria pectidea</i> (DC.) Harv.	Y	Namibia, northern desert fringe; Namibia, southern Nama-Karoo

***Quartinia hecuba* (Richards), described from 13 females and four males, Western Cape and KwaZulu-Natal**

No flower-visiting records.

***Quartinia helena* (Richards), described from 11 females, Western Cape**

No flower-visiting records.

Quartinia helichrysi* (Richards), Lesotho*Asteraceae, eight females**

<i>Helichrysum fruticans</i> (L.) D.Don		Lesotho (Jacot Guillarmod)
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***Quartinia hetaira* (Richards), described from three females and two males, Western Cape**

No flower-visiting records.

***Quartinia hypatica* Richards, described from 14 males, Northern Cape**

No flower-visiting records.

***Quartinia interrupta* Turner, six females, three males seen by Richards (1962), Western Cape, Eastern Cape and Namibia**

No flower-visiting records.

***Quartinia iphigenia* (Richards), described from five females, Namibia**

No flower-visiting records.

Quartinia jocasta* Richards, Northern Cape and Namibia*Aizoaceae: non-Mesembryanthema, many**

<i>Galenia filiformis</i> (Thunb.) N.E.Br.	not given	Namaqualand, Klipkoppe (Struck)
<i>Galenia secunda</i> (L.f.) Sond.	YG	Namaqualand, northern Klipkoppe
<i>Galenia</i> sp.	Pi	Namaqualand, Richtersveld

Aizoaceae: Mesembryanthema, one female

'mesem'	PiW	Namibia, 'Richtersveld'
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Asteraceae, many

<i>Helichrysum herniarioides</i> DC.	W	Namaqualand, Richtersveld; Namibia, 'Richtersveld'
<i>Leysera gnaphalodes</i> (L.) L.	Y	Namaqualand, Klipkoppe
<i>Leysera tenella</i> DC.	Y	Namaqualand, northern
<i>Tripteris microcarpa</i> Harv.	Y	Namibia, 'Richtersveld'

Boraginaceae (Hydrophyllaceae), one male

<i>Codon royenii</i> L.	W	Namaqualand, Richtersveld
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Campanulaceae, four females

<i>Wahlenbergia namaquana</i> Sond.	Pi	Namaqualand, Klipkoppe
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Quartinia laeta* von Schulthess, Namaqualand, Northern Cape and Namibia*Aizoaceae: Mesembryanthema, four males**

<i>Drosanthemum</i> sp.	Pi	Namaqualand, sandveld
<i>Conicosia</i> sp.	Y	Namaqualand, sandveld
<i>Stoeberia</i> sp.	Pi	Bushmanland, western

***Quartinia lamellata* Gess, widespread in western Namibia**

No flower-visiting records.

***Quartinia latona* (Richards), described from one female, Western Cape**

No flower-visiting records.

***Quartinia maerens* von Schulthess, 16 females, four males seen by Richards (1962), Western Cape**

No flower-visiting records.

***Quartinia matabele* Turner, four females, two males seen by Richards (1962), Zimbabwe**

No flower-visiting records.

***Quartinia media* von Schulthess, southwestern Western Cape**

Aizoaceae: Mesembryanthema, number of records not given

'Mesembryanthemum'	YW	(Turner)
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***Quartinia medusa* Richards, described from one female, one male, Namibia**

No flower-visiting records.

Quartinia metallescens* von Schulthess, eastern Northern Cape and Lesotho*Asteraceae, four females**

<i>Gazania linearis</i> (Thunb.) Druce	Y	Lesotho (Jacot Guillarmod)
<i>Gazania</i> sp.	not given	Lesotho (Jacot Guillarmod)
<i>Helichrysum</i> sp.	not given	Lesotho (Jacot Guillarmod)

***Quartinia metope* (Richards), described from three females, Namibia**

No flower-visiting records.

Quartinia minima* von Schulthess, Namibia*Aizoaceae: non-Mesembryanthema, many**

<i>Galenia papulosa</i> (Eckl. & Zeyh.) Sond.	Y	Namibia, northern coast
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Aizoaceae: Mesembryanthema, three females, one male

<i>Brownanthus kuntzei</i> (Schinz) Ihlenf. & Bittrich	W	Namibia, northern coast
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Asteraceae, one female

<i>Tripteris microcarpa</i> Harv.	Y	Namibia, northern coast
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Zygophyllaceae, two females

<i>Zygophyllum simplex</i> L.	Y	Namibia, northern coast
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***Quartinia minuscula* (Turner), six females seen by Richards (1962), Eastern Cape**

No flower-visiting records.

***Quartinia multiplicata* (Richards), described from 44 females, three males, Western Cape**

No flower-visiting records.

***Quartinia namaqua* Gess, Western Cape and Northern Cape, nesting in snail shells**

Aizoaceae: Mesembryanthema, one female

<i>Conicosia</i> sp.	Y	northwestern Olifants River Valley, sand-veld
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***Quartinia namaquensis* Gess, Northern Cape, nesting in snail shells**

No flower-visiting records.

***Quartinia niveopicta* von Schulthess, Western Cape and Eastern Cape**

Aizoaceae: Mesembryanthema, number of records not given

'Mesembryanthemum'	not given	(Turner)
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Plumbaginaceae, one female

<i>Limonium</i> sp.	V	Tankwa Karoo, southern
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***Quartinia obibensis* Gess, Western Cape, Northern Cape and Namibia, nesting in snail shells**

Aizoaceae: Mesembryanthema, one male

<i>Drosanthemum</i> sp.	Pi	Namibia, 'Richtersveld'
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***Quartinia ochraceopicta* von Schulthess, Namibia**

Aizoaceae: Mesembryanthema, number of records not given

'Mesembryanthemum'	W	Namibia, southwestern (Turner)
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***Quartinia paradoxa* Brauns, described from one male, Eastern Cape**

No flower-visiting records.

Quartinia parcepunctata* Richards, Western Cape*Campanulaceae, many**

<i>Microcodon sparsiflorum</i> A.DC.	V	Olifants River Valley
<i>Wahlenbergia</i> cf. <i>constricta</i> Brehmer	V	west of Olifants River Valley
<i>Wahlenbergia ecklonii</i> H.Buek	V	Western Cape, Theron's Pass
<i>Wahlenbergia paniculata</i> (Thunb.) A.DC.	V	Olifants River Valley

***Quartinia perone* Richards, described from one female, Western Cape**

No flower-visiting records.

***Quartinia persephone* Richards, Western Cape and Northern Cape**

Aizoaceae: Mesembryanthema, one female

<i>Prenia pallens</i> (Aiton) N.E.Br.	WPi	Olifants River Valley
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Asteraceae, four females

<i>Athanasia trifurcata</i> (L.) L.	Y	west of Olifants River Valley
<i>Leysera gnaphalodes</i> (L.) L.	Y	Namaqualand, southeastern
<i>Senecio</i> sp.	Y	Namaqualand, southeastern

Campanulaceae, nine females, three males

<i>Microcodon sparsiflorum</i> A.DC.	V	Olifants River Valley
<i>Wahlenbergia paniculata</i> (Thunb.) Druce	V	Olifants River Valley
<i>Wahlenbergia</i> sp.	V	Namaqualand, southeastern

***Quartinia philomela* (Richards), described from five females, western Northern Cape**

No flower-visiting records.

***Quartinia phoebe* (Richards), described from five males, Western Cape**

No flower-visiting records.

***Quartinia pluto* Richards, described from one female, Western Cape**

No flower-visiting records.

Quartinia poecila* von Schulthess, Northern Cape and Namibia*Aizoaceae: Mesembryanthema, many**

<i>Brownanthus</i> sp.	Pi	Namibia, northern coast
<i>Conicosia</i> sp.	Y	Northern Cape, coast
<i>Drosanthemum</i> sp.	Pi	Northern Cape, coast
<i>Phyllobolus oculatus</i> (N.E.Br.) Gerbaulet	Y	Namibia, Sperrgebiet

Aizoaceae: non-Mesembryanthema, two females

<i>Galenia papulosa</i> (Eckl. & Zeyh.) Sond.	Pi	Namibia, northern coast
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Asteraceae, many

<i>Berkheya</i> sp.		Namibia, northern coast (Turner)
<i>Dimorphotheca polyptera</i> DC.	Y	Namibia, Sperrgebiet
<i>Oncosiphon grandiflorum</i> (Thunb.) Källersjö	Y	Namibia, Sperrgebiet
<i>Pteronia pomonae</i> Merxm.	Y	Namibia, Sperrgebiet
<i>Tripteris crassifolia</i> O.Hoffm.	Y	Namibia, Sperrgebiet
'composite'	Y	Northern Cape, coast

Neuradaceae, very many

<i>Grielum sinuatum</i> Licht. ex Burch.	Y	Namibia, Sperrgebiet; Namibia, south-western desert fringe
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Scrophulariaceae, one female

<i>Polycarena</i> cf. <i>collina</i> Hiern	W	Northern Cape, sandveld
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Zygophyllaceae, three females, one male

<i>Zygophyllum clavatum</i> Schltr. & Diels	W	Namibia, southern coast
<i>Zygophyllum stapfii</i> Schinz	W	Namibia, northern coast

***Quartinia propinqua* von Schulthess, Western Cape, Northern Cape and Namibia**

Aizoaceae: non-Mesembryanthema, one female, one male

<i>Galenia africana</i> L.	W	Namibia, northern coast
<i>Sesuvium sesuvioides</i> (Fenzl.) Verdc.	PuPi	Namibia, northern desert

Aizoaceae: Mesembryanthema, one female

'mesemb'	W	Namibia, southwestern desert fringe
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Asteraceae, very many

<i>Berkheya schinzii</i> O.Hoffm.	Y	Namibia southwestern desert fringe; Namibia, Sperrgebiet
<i>Berkheya</i> cf. <i>spinosa</i> (L.f.) Druce	Y	Nama-Karoo, southern
<i>Didelta carnosa</i> (L.f.) Aiton	Y	Namaqualand, Richtersveld
<i>Dimorphotheca polyptera</i> DC.	Y	Namibia, southern desert fringe
<i>Emilia marlothiana</i> (O.Hoffm.) C.Jeffrey	W	Namibia, northwestern
<i>Felicia anthemoides</i> (Hiern) C.Jeffrey	BV	Namibia, northwestern
<i>Gazania</i> sp.	Y	Nama-Karoo, western
<i>Geigeria ornativa</i> O.Hoffm.	Y	Namibia, southern Nama-Karoo
<i>Hirpicium echinus</i> Less.	Y	Namibia, southern desert fringe
<i>Hirpicium</i> sp.	Y	Namibia, northern desert fringe
<i>Leysera gnaphalodes</i> (L.) L.	Y	Namaqualand, southeast
<i>Leysera</i> sp.	Y	Namibia, southwestern desert fringe
<i>Osteospermum sensu lato</i>	Y	Namaqualand, Richtersveld
<i>Othonna sparsiflora</i> (S. Moore) B.Nord.	Y	Namibia, southwestern
<i>Senecio</i> cf. <i>niveus</i> Less.	W	Namaqualand, southeast
<i>Tripteris crassifolia</i> O.Hoffm.	Y	Namibia, southwestern
<i>Tripteris microcarpa</i> Harv.	Y	Namibia, northern desert; Namibia 'Richtersveld'
<i>Tripteris sinuata</i> DC.	Y	Namibia, Sperrgebiet
'daisy'	Y	Bushmanland
'daisy'	Y	Namibia, Sperrgebiet

Brassicaceae (Capparaceae), one female

<i>Cleome paxii</i> (Schinz) Gilg & Ben.	Y	Namaqualand, Richtersveld
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Neuradaceae, two females

<i>Grielum grandiflorum</i> (L.) Druce	Y	Namaqualand, Richtersveld
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Vahliaceae, one female

<i>Vahlia capensis</i> (L.f.) Thunb.	Y	Namibia, southern Nama-Karoo
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***Quartinia prosperina* Richards, described from one female, Northern Cape**

No flower-visiting records.

Quartinia punctulata* von Schulthess, southwestern Namibia and Western Cape*Aizoaceae: Mesembryanthema, solely**

<i>Mesembryanthemum crystallinum</i> L.	YW	southwestern Namibia (Turner)
<i>Mesembryanthemum crystallinum</i> L.	YW	southern Nama-Karoo (Turner)
<i>Mesembryanthemum crystallinum</i> L.	YW	southwestern Western Cape (Turner)

***Quartinia refugicola* Gess, Northern Cape and Namibia, nesting in snail shells**

Aizoaceae: Mesembryanthema, three females

<i>Phyllobolus oculatus</i> (N.E.Br.) Gerbaulet	PiO	Namibia, Sperrgebiet
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Asteraceae, many

<i>Dimorphotheca polyptera</i> DC.	Y	Namibia, Sperrgebiet
<i>Felicia</i> sp.	B	Namibia, 'Richtersveld'
<i>Foveolina dichotoma</i> (DC.) Källersjö	Y	Namibia, Sperrgebiet
<i>Hirpicium</i> sp.	Y	Namibia, 'Richtersveld'
<i>Leysera tenella</i> DC.	Y	southern Namibia, desert fringe
<i>Pteronia</i> sp.	Y	Namibia, Sperrgebiet
<i>Tripteris</i> sp.	Y	Namibia, 'Richtersveld'

Geraniaceae, one female

<i>Sarcocaulon</i> sp.	Pi	Namibia, Sperrgebiet
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Neuradaceae, three females

<i>Grielum</i> sp.	Y	Namibia, 'Richtersveld'
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Zygophyllaceae, six female, one male

<i>Zygophyllum clavatum</i> Schltr. & Diels	W	Namibia, Sperrgebiet
<i>Zygophyllum simplex</i> L.	Y	Namibia, Sperrgebiet

Quartinia senecionis* (Richards), Free State and Lesotho*Asteraceae, many**

<i>Felicia muricata</i> (Thunb.) Nees	BV	Lesotho (Jacot Guillarmod)
<i>Felicia muricata</i> (Thunb.) Nees	BV	eastern Free State, four sites
<i>Felicia muricata</i> (Thunb.) Nees	BV	northwestern Eastern Cape
<i>Gazania</i> sp.	not given	Lesotho (Jacot Guillarmod)
<i>Pentzia incana</i> (Thunb.) Kuntze	Y	eastern Free State
<i>Senecio laevigatus</i> Thunb.	not given	Free State (Jacot Guillarmod)

***Quartinia signata* von Schulthess, Eastern Cape**

Aizoaceae: Mesembryanthema, number of records not given

'Mesembryanthemum'	not given	locality not given (Turner)
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***Quartinia signatifrons* Turner, 13 females, nine males seen by Richards (1962), Western Cape and Eastern Cape**

No flower-visiting records.

***Quartinia striata* (Richards), described from two females, Northern Cape**

No flower-visiting records.

Quartinia strucki* Gess, Knersvlakte Namaqualand*Aizoaceae: Mesembryanthema, many**

<i>Argyroderma fissum</i> (Haw.) L.Bolus	W	Namaqualand, Knersvlakte (Struck)
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***Quartinia tarsata* (Richards), Eastern Cape and Northern Cape**

Aizoaceae: Mesembryanthema, 15 females and males combined

<i>Delosperma acuminatum</i> L.Bolus		Nama-Karoo, southeastern
<i>Drosanthemum hispidum</i> (L.) Schwantes	Pi	Nama-Karoo, southeastern

Asteraceae, four females, one male

<i>Berkheya fruticosa</i> (L.) Ehrh.	Y	Namaqualand, southeast
<i>Berkheya</i> sp.	Y	Nama-Karoo, western
<i>Gazania</i> sp.	Y	Nama-Karoo, western

Scrophulariaceae, many

<i>Aptosimum procumbens</i> (Lehm.) Steud.	BV	Nama-Karoo, southeastern
<i>Peliostomum leucorrhizum</i> E.Mey. ex Benth.	BV	Kalahari, southern
<i>Peliostomum leucorrhizum</i> E.Mey. ex Benth.	BV	Nama-Karoo, northern
<i>Peliostomum leucorrhizum</i> E.Mey. ex Benth.	BV	Nama-Karoo, western
<i>Peliostomum virgatum</i> E.Mey. ex Benth.	PV	Namaqualand, Klipkoppe

***Quartinia titania* (Richards), described from 32 females, one male, Western Cape**

No flower-visiting records.

***Quartinia turneri* (von Schulthess), Northern Cape and Namibia**

Aizoaceae: Mesembryanthema, one female

'mesemb'	Pi	Namaqualand, Richtersveld
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Aizoaceae: non-Mesembryanthema, many

<i>Galenia africana</i> L.	W	Namibia, northern desert
<i>Galenia</i> sp.	Pi	Namaqualand, Richtersveld
<i>Trianthema parvifolia</i> E.Mey. ex Sond.	Pi	Namibia, southern Nama-Karoo

Asteraceae, many

<i>Foveolina albida</i> (DC.) Källersjö	Y	Namibia, 'Richtersveld'
<i>Leysera tenella</i> DC.	Y	Namaqualand, Richtersveld

***Quartinia vagepunctata* von Schulthess, Western Cape, Northern Cape and Namibia, nesting in horizontal ground**

Aizoaceae: non-Mesembryanthema, one female

<i>Galenia</i> sp.	Pi	Namaqualand, Klipkoppe
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Asteraceae, very many and provision

<i>Cotula leptalea</i> DC.	Y	Namaqualand, southeast
<i>Cotula</i> sp.	Y	Namaqualand, Klipkoppe
<i>Cotula</i> sp.	Y	Namaqualand, southeast
<i>Helichrysum herniarioides</i> DC.	W	Namaqualand, Richtersveld
<i>Helichrysum herniarioides</i> DC.	W	Namibia, 'Richtersveld'
<i>Leysera gnaphalodes</i> (L.) L.	Y	Namaqualand, Klipkoppe
<i>Leysera gnaphalodes</i> (L.) L.	Y	Namaqualand, southeast



<i>Leysera tenella</i> DC.	Y	Namaqualand, Klipkoppe
<i>Leysera tenella</i> DC.	Y	Namaqualand, Richtersveld
<i>Oncosiphon suffruticosa</i> (L.) Källersjö	Y	Namaqualand, Klipkoppe
<i>Oncosiphon suffruticosa</i> (L.) Källersjö	Y	Namaqualand, southeast
<i>Tripteris microcarpa</i> Harv.	Y	'Richtersveld', Namibia
<i>Osteospermum sensu lato</i> sp.	Y	Namaqualand, southeast
<i>Relhania pumila</i> Thunb.	Y	Namaqualand, southeast
<i>Senecio</i> cf. <i>niveus</i> Less.	W	Namaqualand, southeast

Fabaceae, one male

<i>Lebeckia sericea</i> Thunb.	Y	Namaqualand, Klipkoppe
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***Quartinia vexillata* Gess, Northern Cape and Namibia**

Aizoaceae, 16 females, one male

<i>Cephalophyllum</i> sp.	Y	Namibia, southern Sperrgebiet
<i>Drosanthemum</i> sp.	Pi	Namaqualand, Richtersveld, coast
'mesemb'	W	Namaqualand, Richtersveld coast

Asteraceae, two females

<i>Othonna cylindrica</i> (Lam.) DC.	Y	Namibia, southern Sperrgebiet
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***Quartinia waterstoni* (von Schulthess), Western Cape and Northern Cape**

Asteraceae, 19 females, four males

<i>Athanasia trifurcata</i> (L.) L.	Y	Tankwa Karoo, southern
<i>Pentzia suffruticosa</i> (L.) Hutch. ex Merxm.	Y	Tankwa Karoo, southern

***Quartinia* Gess sp. A, Sperrgebiet Namibia**

Asteraceae, very many

<i>Pteronia pomonae</i> Merxm.	Y	Namibia, Sperrgebiet
<i>Relhania</i> sp.	Y	Namibia, Sperrgebiet

***Quartinia* Gess sp. B, Sperrgebiet Namibia**

Aizoaceae: Mesembryanthema, one female

<i>Aridaria</i> sp.	WPi	Sperrgebiet, Namibia
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Asteraceae, many

<i>Pteronia pomonae</i> Merxm.	Y	Sperrgebiet, Namibia
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***Quartinia* Gess sp. C, northwestern Namibia**

No flower-visiting records.

***Quartinia* Gess sp. D, northern Namibia, coast and desert**

Aizoaceae: Mesembryanthema, very many

<i>Brownanthus kuntzei</i> (Schinz.) Ihlenf. & Bittrich	W	Namibia, northern coast
<i>Psilocaulon salicornioides</i> (Pax) Schwantes	W	Namibia, northern coast

Zygophyllaceae, one female

<i>Zygophyllum simplex</i> L.	Y	Namibia, northern desert
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Quartinia Gess sp. E, northern Namibia, coast and desert**Aizoaceae: Mesembryanthema, very many**

<i>Brownanthus kuntzei</i> (Schinz.) Ihlenf. & Bittrich	W	Namibia, northern coast
<i>Psilocalon salicornioides</i> (Pax) Schwantes	W	Namibia, northern coast

Aizoaceae: non-Mesembryanthema, many

<i>Galenia africana</i> L.	W	Namibia, northern desert
<i>Galenia papulosa</i> (Eckl. & Zeyh.) Sond.	Pi	Namibia, northern coast

Amaranthaceae, many

cf. <i>Leucosphaera bainesii</i> (Hook.f.) Gilg	Pi	Namibia, northern desert
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Asteraceae, many

<i>Myxopappus hereroensis</i> (O.Hoffm.) Källersjö	Y	Namibia, northern coast
<i>Tripteris microcarpa</i> Harv.	Y	Namibia, northern desert
<i>Tripteris microcarpa</i> Harv.	Y	Namibia, northern coast

Boraginaceae, two females

<i>Heliotropium tubulosum</i> E.Mey. ex DC.	W	Namibia, northern desert
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Cucurbitaceae, one male

'cucurbit'	Y	Namibia, northern desert
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Fabaceae: Papilionoideae, two females

<i>Indigofera</i> sp.	Pi	Namibia, northern desert
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Fabaceae: Caesalpinoideae, one female

<i>Adenolobus pechuelii</i> (Kuntze) Torre & Hilc.	YO	Namibia, northern desert
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Zygophyllaceae, many

<i>Zygophyllum simplex</i> L.	Y	Namibia, northern desert
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Quartinia Gess sp. F, Sperrgebiet Namibia**Malvaceae (Sterculiaceae), many**

<i>Hermannia gariepina</i> Eckl. & Zeyh.	Pi	Namibia, Sperrgebiet
<i>Hermannia macra</i> Schltr.	Y	Namibia, Sperrgebiet

Geraniaceae, one female

<i>Sarcocaulon patersonii</i> (DC.) G.Don	Pi	Namibia, Sperrgebiet
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Appendix 3

Flowers visited by pollen wasps in southern Africa

The plant families are arranged in the same order as in the chapter on flower visitation.

Dicotyledons

Aizoaceae: non-Mesembryanthema, many records and provision

<i>Galenia africana</i> L.	<i>Quartinia propinqua</i> von Schulthess; <i>Quartinia</i> Gess sp. E; <i>Quartinia turneri</i> (von Schulthess)
<i>Galenia filiformis</i> (Thunb.) N.E.Br.	<i>Quartinia jocasta</i> Richards
<i>Galenia papulosa</i> (Eckl. & Zeyh.) Sond.	<i>Quartinia minima</i> von Schulthess; <i>Quartinia poecila</i> von Schulthess; <i>Quartinia</i> Gess sp. E
<i>Galenia sarcophylla</i> Fenzl	<i>Jugurtia braunsi</i> (von Schulthess)
<i>Galenia secunda</i> (L.f.) Sond.	<i>Quartinia jocasta</i> Richards
<i>Galenia</i> spp.	<i>Quartinia flava</i> (Richards); <i>Quartinia jocasta</i> Richards; <i>Quartinia turneri</i> (von Schulthess); <i>Quartinia vagepunctata</i> von Schulthess
<i>Sesuvium sesuvioides</i> (Fenzl) Verdc.	<i>Priscomasaris namibiensis</i> Gess; <i>Ceramius damarinus</i> Turner; <i>Quartinia propinqua</i> von Schulthess
<i>Tetragonia</i> sp.	<i>Jugurtia braunsi</i> (von Schulthess)
<i>Trianthema hereroensis</i> Schinz	<i>Quartinia albopicta</i> (Richards); <i>Quartinia femorata</i> Gess
<i>Trianthema parvifolia</i> E.Mey. ex Sond.	<i>Priscomasaris namibiensis</i> Gess; <i>Quartinia flava</i> (Richards); <i>Quartinia turneri</i> (von Schulthess)

Aizoaceae: Mesembryanthema

<i>Apatesia</i> sp.	<i>Celonites latitarsis</i> Gess
<i>Argyroderma fissum</i> (Haw.) L.Bolus	<i>Quartinia strucki</i> Gess
<i>Aridaria dyeri</i> L.Bolus	<i>Ceramius capicola</i> Brauns; <i>Ceramius linearis</i> Klug
<i>Aridaria plenifolia</i> (N.E.Br.) Stearn	<i>Ceramius capicola</i> Brauns; <i>Ceramius linearis</i> Klug
<i>Aridaria</i> sp.	<i>Ceramius cerceriformis</i> de Saussure; <i>Ceramius lichtensteinii</i> (Klug); <i>Quartinia</i> Gess sp. B
<i>Brownanthus kuntzei</i> (Schinz) Ihlenf. & Bittrich	<i>Quartinia minima</i> von Schulthess; <i>Quartinia</i> Gess sp. D; <i>Quartinia</i> Gess sp. E
<i>Brownanthus</i> sp.	<i>Quartinia poecila</i> von Schulthess
<i>Cephalophyllum</i> sp.	<i>Quartinia vexillata</i> Gess
<i>Conicosia</i> sp.	<i>Jugurtia braunsi</i> (von Schulthess); <i>Celonites bergenwahliae</i> Gess; <i>Celonites latitarsis</i> Gess; <i>Celonites wahlenbergiae</i> Gess; <i>Quartinia bonaespei</i> Gess; <i>Quartinia laeta</i> von Schulthess; <i>Quartinia namaqua</i> Gess; <i>Quartinia poecila</i> von Schulthess
<i>Delosperma acuminatum</i> L.Bolus	<i>Quartinia tarsata</i> (Richards)
<i>Drosanthemum floribundum</i> (Haw.) Schwantes	<i>Ceramius capicola</i> Brauns; <i>Ceramius linearis</i> Klug
<i>Drosanthemum hispidum</i> (L.) Schwantes	<i>Jugurtia braunsi</i> (von Schulthess); <i>Jugurtia nigrifrons</i> Gess; <i>Quartinia tarsata</i> (Richards)
<i>Drosanthemum parvifolium</i> (Haw.) Schwantes	<i>Jugurtia confusa</i> Richards

<i>Drosanthemum</i> sp.	<i>Ceramius bicolor</i> (Thunberg); <i>Jugurtia calcarata</i> Richards; <i>Quartinia bonaespei</i> Gess; <i>Quartinia conchicola</i> Gess; <i>Quartinia diana</i> (Richards); <i>Quartinia laeta</i> von Schulthess; <i>Quartinia obibensis</i> Gess; <i>Quartinia poecila</i> von Schulthess; <i>Quartinia vexillata</i> Gess
<i>Herrea</i> sp.	<i>Jugurtia braunsi</i> (von Schulthess)
<i>Leipoldtia constricta</i> (L.Bolus) L.Bolus	<i>Jugurtia braunsi</i> (von Schulthess); <i>Jugurtia nigrifrons</i> Gess
<i>Malephora</i> sp.	<i>Ceramius linearis</i> Klug
<i>Mesembryanthemum aitonis</i> Jacq.	<i>Ceramius lichtensteinii</i> (Klug); <i>Ceramius linearis</i> Klug
<i>Mesembryanthemum crystallinum</i> L.	<i>Quartinia punctulata</i> von Schulthess
<i>Mesembryanthemum pallens</i> (Aiton) N.E.Br.	<i>Ceramius cerceriformis</i> de Saussure
' <i>Mesembryanthemum</i> ' sensu Turner	<i>Quartinia atra</i> von Schulthess; <i>Quartinia capensis</i> (Kohl); <i>Quartinia niveopicta</i> von Schulthess; <i>Quartinia ochraceopicta</i> von Schulthess; <i>Quartinia signata</i> von Schulthess
<i>Mestoklema tuberosum</i> (L.) N.E.Br.	<i>Ceramius capicola</i> Brauns
<i>Phyllobolus oculatus</i> (N.E.Br.) Gerbaulet	<i>Quartinia poecila</i> von Schulthess; <i>Quartinia refugicola</i> Gess
<i>Phyllobolus</i> cf. <i>splendens</i> (L.) Gerbaulet	<i>Ceramius beyeri</i> Brauns; <i>Ceramius lichtensteinii</i> (Klug)
<i>Platythya haeckeliana</i> (A.Berger) N.E.Br.	<i>Ceramius capicola</i> Brauns
<i>Prenia pallens</i> (Aiton) N.E.Br.	<i>Ceramius beyeri</i> Brauns; <i>Ceramius bicolor</i> (Thunberg); <i>Ceramius peringueyi</i> Brauns; <i>Ceramius socius</i> Turner; <i>Jugurtia calcarata</i> Richards; <i>Celonites capensis</i> Brauns; <i>Celonites wahlenbergiae</i> Gess; <i>Quartinia persephone</i> Richards
<i>Psilocaulon</i> cf. <i>absimile</i> N.E.Br.	<i>Ceramius linearis</i> Klug
<i>Psilocaulon acutisepalum</i> (A.Berger) N.E.Br.	<i>Ceramius peringueyi</i> Brauns
<i>Psilocaulon junceum</i> (Haw.) Schwantes	<i>Ceramius peringueyi</i> Brauns; <i>Ceramius socius</i> Turner; <i>Celonites wahlenbergiae</i> Gess
<i>Psilocaulon salicornioides</i> (Pax) Schwantes	<i>Quartinia</i> Gess sp. D; <i>Quartinia</i> Gess sp. E
<i>Psilocaulon</i> cf. <i>utile</i> L.Bolus	<i>Ceramius bicolor</i> (Thunberg)
<i>Psilocaulon</i> sp.	<i>Quartinia diana</i> (Richards)
<i>Ruschia</i> sp.	<i>Ceramius capicola</i> Brauns; <i>Ceramius lichtensteinii</i> (Klug); <i>Ceramius linearis</i> Klug; <i>Jugurtia braunsi</i> (von Schulthess)
<i>Stoeberia</i> sp.	<i>Quartinia laeta</i> (von Schulthess)
'mesemb'	<i>Quartinia jocasta</i> Richards; <i>Quartinia propinqua</i> von Schulthess; <i>Quartinia turneri</i> (von Schulthess); <i>Quartinia vexillata</i> Gess

Molluginaceae

<i>Gisekia africana</i> (Lour.) Kuntze	<i>Priscomasaris namibiensis</i> Gess; <i>Jugurtia mandibulata</i> Gess
<i>Limeum argute-carinatum</i> Wawra & Peyr.	<i>Priscomasaris namibiensis</i> Gess
<i>Limeum myosotis</i> H.Walter	<i>Priscomasaris namibiensis</i> Gess
<i>Limeum sulcatum</i> (Klotzsch) Hutch.	<i>Priscomasaris namibiensis</i> Gess



Asteraceae

<i>Arctotheca calendula</i> (L.) Levyns	<i>Ceramius braunsi</i> Turner; <i>Ceramius nigripennis</i> de Saussure; <i>Jugurtia braunsi</i> (von Schulthess)
<i>Arctotis laevis</i> Thunb.	<i>Ceramius braunsi</i> Turner; <i>Ceramius nigripennis</i> de Saussure
<i>Athanasia trifurcata</i> (L.) L.	<i>Ceramius braunsi</i> Turner; <i>Ceramius metanotalis</i> Richards; <i>Ceramius toriger</i> von Schulthess; <i>Jugurtia braunsiella</i> (von Schulthess); <i>Jugurtia turneri</i> (von Schulthess); <i>Masarina mixta</i> Richards; <i>Quartinia persephone</i> Richards; <i>Quartinia watersoni</i> (von Schulthess)
<i>Athanasia</i> sp.	<i>Quartinia cylene</i> (Richards)
<i>Berkheya canescens</i> DC.	<i>Ceramius rex</i> de Saussure
<i>Berkheya carlinifolia</i> (DC.) Roessler	<i>Ceramius caffer</i> de Saussure
<i>Berkheya fruticosa</i> (L.) Ehrh.	<i>Ceramius braunsi</i> Turner; <i>Ceramius nigripennis</i> de Saussure; <i>Ceramius toriger</i> von Schulthess; <i>Celonites promontorii</i> Brauns; <i>Quartinia tarsata</i> (Richards)
<i>Berkheya heterophylla</i> (Thunb.) O.Hoffm.	<i>Celonites capensis</i> Brauns
<i>Berkheya onobromoides</i> (DC.) O.Hoffm. & Muschl.	<i>Ceramius nigripennis</i> de Saussure; <i>Ceramius rex</i> de Saussure
<i>Berkheya schinzii</i> O.Hoffm.	<i>Quartinia propinqua</i> von Schulthess
<i>Berkheya</i> cf. <i>spinosa</i> (L.f.) Druce	<i>Celonites promontorii</i> Brauns; <i>Celonites wheeleri</i> Brauns; <i>Quartinia propinqua</i> von Schulthess
<i>Berkheya</i> sp.	<i>Ceramius caffer</i> de Saussure; <i>Ceramius capicola</i> Brauns; <i>Quartinia poecila</i> von Schulthess
<i>Cotula leptalea</i> DC.	<i>Quartinia vagepunctata</i> von Schulthess
'cotula'	<i>Quartinia flava</i> (Richards)
<i>Didelta carnosus</i> (L.f.) Aiton	<i>Quartinia propinqua</i> von Schulthess
<i>Dimorphotheca polyptera</i> DC.	<i>Quartinia poecila</i> von Schulthess; <i>Quartinia refugicola</i> Gess
<i>Dimorphotheca sinuata</i> DC.	<i>Ceramius nigripennis</i> de Saussure
<i>Emilia marlothiana</i> (O.Hoffm.) C.Jeffrey	<i>Quartinia propinqua</i> von Schulthess
<i>Felicia anthemoides</i> (Hiern) C.Jeffrey	<i>Quartinia propinqua</i> von Schulthess
<i>Felicia muricata</i> (Thunb.) Nees	<i>Quartinia basuto</i> (Richards); <i>Quartinia senecionis</i> (Richards)
<i>Felicia</i> sp.	<i>Jugurtia braunsiella</i> (von Schulthess); <i>Quartinia diana</i> (Richards); <i>Quartinia refugicola</i> Gess
<i>Foveolina dichotoma</i> (DC.) Källersjö	<i>Quartinia refugicola</i> Gess; <i>Quartinia turneri</i> (von Schulthess)
<i>Gazania linearis</i> (Thunb.) Druce	<i>Quartinia metallescens</i> von Schulthess
<i>Gazania</i> sp.	<i>Quartinia propinqua</i> von Schulthess; <i>Quartinia senecionis</i> (Richards); <i>Quartinia tarsata</i> (Richards)
<i>Geigeria ornativa</i> O.Hoffm.	<i>Quartinia geigeriae</i> Gess; <i>Quartinia propinqua</i> von Schulthess
<i>Geigeria pectidea</i> (DC.) Harv.	<i>Jugurtia tibialis</i> Gess; <i>Quartinia geigeriae</i> Gess
<i>Helichrysum fruticans</i> (L.) D.Don	<i>Quartinia helichrysi</i> (Richards)
<i>Helichrysum herniarioides</i> DC.	<i>Quartinia jocasta</i> Richards; <i>Quartinia vagepunctata</i> von Schulthess
<i>Helichrysum</i> sp.	<i>Celonites wahlenbergiae</i> Gess; <i>Quartinia metallescens</i> von Schulthess
<i>Hirpicium alienatum</i> (Thunb.) Druce	<i>Ceramius nigripennis</i> de Saussure

<i>Hirpicium echinus</i> Less.	<i>Quartinia propinqua</i> von Schulthess
<i>Hirpicium</i> sp.	<i>Quartinia refugicola</i> Gess
<i>Lasiospermum bipinnata</i> (Thunb.) Druce	<i>Jugurtia braunsiella</i> (von Schulthess)
<i>Leysera gnaphalodes</i> (L.) L.	<i>Ceramius nigripennis</i> de Saussure; <i>Jugurtia braunsi</i> (von Schulthess); <i>Jugurtia eburnea</i> (Turner); <i>Jugurtia tigrina</i> Gess; <i>Quartinia cylene</i> (Richards); <i>Quartinia jocasta</i> Richards; <i>Quartinia persephone</i> Richards; <i>Quartinia propinqua</i> von Schulthess; <i>Quartinia vagepunctata</i> von Schulthess
<i>Leysera tenella</i> DC.	<i>Quartinia artemis</i> Richards; <i>Quartinia jocasta</i> Richards; <i>Quartinia turneri</i> (von Schulthess), <i>Quartinia vagepunctata</i> von Schulthess
<i>Myxopappus hereroensis</i> (O.Hoffm.) Källersjö	<i>Quartinia</i> Gess sp. E
<i>Ondetia linearis</i> Benth.	<i>Jugurtia elegans</i> Gess
<i>Ondetia ornativa</i> O.Hoffm.	<i>Jugurtia tibialis</i> Gess
<i>Oncosiphon grandiflorum</i> (Thunb.) Källersjö	<i>Ceramius braunsi</i> Turner; <i>Quartinia poecila</i> von Schulthess
<i>Oncosiphon suffruticosa</i> (L.) Källersjö	<i>Quartinia vagepunctata</i> von Schulthess
<i>Osteospermum oppositifolium</i> (Aiton) Norl.	<i>Jugurtia eburnea</i> (Turner)
<i>Osteospermum</i> sp.	<i>Jugurtia koeroegabensis</i> Gess; <i>Masarina roberti</i> Gess; <i>Celonites capensis</i> Brauns; <i>Quartinia propinqua</i> von Schulthess
<i>Othonna cylindrica</i> (Lam.) DC.	<i>Quartinia vexillata</i> Gess
<i>Othonna sparsiflora</i> (S.Moore) B.Nord.	<i>Quartinia propinqua</i> von Schulthess
<i>Pentzia incana</i> (Thunb.) Kuntze	<i>Ceramius capicola</i> Brauns; <i>Jugurtia affkeni</i> (du Buysson); <i>Jugurtia braunsiella</i> (von Schulthess); <i>Quartinia senecionis</i> (Richards)
<i>Pentzia suffruticosa</i> (L.) Hutch. ex Merxm.	<i>Ceramius nigripennis</i> de Saussure; <i>Jugurtia braunsi</i> (von Schulthess); <i>Jugurtia calcarata</i> Richards; <i>Quartinia waterstoni</i> (von Schulthess)
<i>Pteronia divaricata</i> (P.J.Bergius) Less.	<i>Ceramius braunsi</i> Turner; <i>Ceramius toriger</i> Schulthess; <i>Jugurtia braunsi</i> (von Schulthess); <i>Celonites promontorii</i> Brauns
<i>Pteronia</i> cf. <i>divaricata</i> (P.J.Bergius) Less.	<i>Jugurtia braunsiella</i> (von Schulthess); <i>Jugurtia nigrifrons</i> Gess
<i>Pteronia incana</i> (Burm.) DC.	<i>Ceramius jacoti</i> Richards; <i>Ceramius nigripennis</i> de Saussure; <i>Jugurtia braunsi</i> (von Schulthess)
<i>Pteronia pomonae</i> Merxm.	<i>Quartinia poecila</i> von Schulthess; <i>Quartinia</i> Gess sp. A; <i>Quartinia</i> Gess sp. B
<i>Pteronia</i> sp.	<i>Ceramius lichtensteinii</i> (Klug); <i>Ceramius rex</i> de Saussure; <i>Jugurtia koeroegabensis</i> Gess; <i>Quartinia refugicola</i> Gess
<i>Relhania pumila</i> (L.f.) Thunb.	<i>Quartinia cylene</i> (Richards); <i>Quartinia vagepunctata</i> von Schulthess
<i>Relhania</i> sp.	<i>Quartinia</i> Gess sp. A
<i>Senecio arenarius</i> Thunb.	<i>Jugurtia codoni</i> Gess
<i>Senecio</i> cf. <i>arenarius</i> Thunb.	<i>Celonites bergenwahliae</i> Gess
<i>Senecio burchellii</i> DC.	<i>Jugurtia braunsiella</i> (von Schulthess); <i>Jugurtia discrepans</i> Brauns
<i>Senecio</i> cf. <i>cinerascens</i> Aiton	<i>Ceramius nigripennis</i> de Saussure
<i>Senecio laevigatus</i> Thunb.	<i>Quartinia senecionis</i> (Richards)



<i>Senecio</i> prob. <i>niveus</i> (Thunb.) Willd.	<i>Jugurtia eburnea</i> (Turner); <i>Quartinia cylene</i> (Richards); <i>Quartinia propinqua</i> von Schulthess; <i>Quartinia vagepunctata</i> von Schulthess
<i>Senecio pterophorus</i> DC.	<i>Ceramius lichtensteinii</i> (Klug); <i>Celonites capensis</i> Brauns
<i>Senecio rosmarinifolius</i> L.f.	<i>Ceramius jacoti</i> Richards; <i>Jugurtia braunsiella</i> (von Schulthess); <i>Jugurtia discrepans</i> Brauns; <i>Jugurtia turneri</i> (von Schulthess); <i>Celonites promontorii</i> Brauns
<i>Senecio</i> sp.	<i>Jugurtia braunsi</i> (von Schulthess); <i>Quartinia persephone</i> Richards
<i>Tripteris crassifolia</i> O.Hoffm.	<i>Quartinia poecila</i> von Schulthess
<i>Tripteris microcarpa</i> Harv.	<i>Quartinia jocasta</i> Richards; <i>Quartinia minima</i> von Schulthess; <i>Quartinia</i> Gess sp. E; <i>Quartinia vagepunctata</i> von Schulthess
<i>Tripteris sinuata</i> DC.	<i>Quartinia propinqua</i> von Schulthess
<i>Tripteris</i> sp.	<i>Quartinia refugicola</i> Gess
'composite'	<i>Masarina mixtoides</i> Gess

Scrophulariaceae, Aptosimeae and other

Aptosimeae	
<i>Anticharis ebracteata</i> Schinz	<i>Celonites michaelsoni</i> von Schulthess
<i>Anticharis inflata</i> Marloth & Engl.	<i>Celonites michaelsoni</i> von Schulthess, <i>Celonites pulcher</i> Gess
<i>Anticharis scoparia</i> (E.Mey. ex Benth.) Hiern. ex Schinz	<i>Celonites pulcher</i> Gess
<i>Aptosimum albomarginatum</i> Marloth & Engl.	<i>Masarina aptosimi</i> Gess
<i>Aptosimum angustifolium</i> Weber & Schinz	<i>Celonites michaelsoni</i> von Schulthess
<i>Aptosimum arenarium</i> Engl.	<i>Celonites michaelsoni</i> von Schulthess
<i>Aptosimum indivisum</i> Burch.	<i>Celonites clypeatus</i> Brauns, <i>Celonites peliostomi</i> Gess, <i>Celonites tumidiscutellatus</i> Gess
<i>Aptosimum lineare</i> Marloth & Engl.	<i>Celonites michaelsoni</i> von Schulthess, <i>Celonites peliostomi</i> Gess
<i>Aptosimum procumbens</i> (Lehm.) Steud.	<i>Celonites andrei</i> Brauns, <i>Celonites clypeatus</i> Brauns, <i>Celonites kalahariensis</i> Gess, <i>Quartinia tarsata</i> (Richards)
<i>Aptosimum spinescens</i> (Thunb.) Weber	<i>Celonites andrei</i> Brauns, <i>Celonites clypeatus</i> Brauns, <i>Celonites michaelsoni</i> von Schulthess, <i>Celonites peliostomi</i> Gess, <i>Celonites tumidiscutellatus</i> Gess
<i>Peliostomum leucorrhizum</i> E.Mey. ex Benth.	<i>Jugurtia koeroegabensis</i> Gess, <i>Celonites tumidiscutellatus</i> Gess, <i>Quartinia diana</i> (Richards), <i>Quartinia tarsata</i> (Richards)
<i>Peliostomum virgatum</i> E.Mey. ex Benth.	<i>Celonites andrei</i> Brauns, <i>Celonites clypeatus</i> Brauns, <i>Celonites peliostomi</i> Gess, <i>Quartinia tarsata</i> (Richards)
<i>Peliostomum</i> sp. Richtersveld	<i>Jugurtia codoni</i> Gess; <i>Masarina mixta</i> Richards; <i>Masarina peliostomi</i> Gess, <i>Celonites clypeatus</i> Brauns, <i>Celonites michaelsoni</i> von Schulthess, <i>Celonites peliostomi</i> Gess

other	
<i>Phyllopodium cuneifolium</i> (L.f.) Benth.	<i>Celonites capensis</i> Brauns
<i>Polycarena cephalophora</i> (Thunb.) Levyns	<i>Jugurtia braunsi</i> (von Schulthess), <i>Celonites wahlenbergiae</i> Gess
<i>Polycarena</i> cf. <i>collina</i> Hiern	<i>Quartinia poecila</i> von Schulthess
<i>Selago dinteri</i> Rolfe	<i>Ceramius damarinus</i> Turner
<i>Selago minutissima</i> Choisy	<i>Jugurtia braunsi</i> (von Schulthess)
<i>Selago verna</i> Hilliard	<i>Jugurtia braunsi</i> (von Schulthess)

Campanulaceae

<i>Lobelia anceps</i> L.f.	<i>Celonites andrei</i> Brauns
<i>Lobelia linearis</i> Thunb.	<i>Celonites lobeliae</i> Gess
<i>Microcodon sparsiflorum</i> A.DC.	<i>Celonites wahlenbergiae</i> Gess, <i>Quartinia parcepunctata</i> Richards, <i>Quartinia persephone</i> Richards
<i>Wahlenbergia annularis</i> A.DC.	<i>Masarina mixta</i> Richards
<i>Wahlenbergia</i> cf. <i>constricta</i> Brehmer	<i>Celonites bergenwahliae</i> Gess, <i>Quartinia parcepunctata</i> Richards
<i>Wahlenbergia ecklonii</i> H.Buek	<i>Celonites capensis</i> Brauns, <i>Quartinia parcepunctata</i> Richards
<i>Wahlenbergia namaquana</i> Sond.	<i>Quartinia jocasta</i> Richards
<i>Wahlenbergia oxyphylla</i> A.DC.	<i>Masarina namaqua</i> Gess, <i>Masarina parvula</i> Gess
<i>Wahlenbergia paniculata</i> (Thunb.) A.DC.	<i>Ceramius socius</i> Turner, <i>Masarina mixta</i> Richards, <i>Celonites wahlenbergiae</i> Gess, <i>Quartinia parcepunctata</i> Richards, <i>Quartinia persephone</i> Richards
<i>Wahlenbergia pilosa</i> H.Buek	<i>Jugurtia braunsi</i> (von Schulthess)
<i>Wahlenbergia</i> cf. <i>prostrata</i> A.DC.	<i>Masarina namaqua</i> Gess
<i>Wahlenbergia psammophila</i> Schltr.	<i>Masarina mixta</i> Richards, <i>Celonites bergenwahliae</i> Gess, <i>Celonites latitarsis</i> Gess, <i>Celonites wahlenbergiae</i> Gess
<i>Wahlenbergia</i> sp.	<i>Masarina mixtoides</i> Gess

Zygophyllaceae

<i>Tribulus</i> sp.	<i>Ceramius damarinus</i> Turner
<i>Zygophyllum clavatum</i> Schltr. & Diels	<i>Quartinia poecila</i> von Schulthess, <i>Quartinia refugicola</i> Gess
<i>Zygophyllum prismatocarpum</i> E.Mey. ex Sond.	<i>Ceramius brevitaris</i> Gess, <i>Jugurtia codoni</i> Gess, <i>Jugurtia koeroegabensis</i> Gess, <i>Masarina mixtoides</i> Gess
<i>Zygophyllum foetidum</i> Schrad. & J.C.Wendl. (= <i>Z. meyeri</i> Sond.)	<i>Jugurtia codoni</i> Gess, <i>Jugurtia koeroegabensis</i> Gess, <i>Masarina mixtoides</i> Gess
<i>Zygophyllum simplex</i> L.	<i>Quartinia minima</i> von Schulthess, <i>Quartinia refugicola</i> Gess, <i>Quartinia</i> Gess sp. D, <i>Quartinia</i> Gess sp. E
<i>Zygophyllum stapfii</i> Schinz	<i>Quartinia poecila</i> von Schulthess

Fabaceae: Papilionoideae: Cape Crotalarieae

<i>Aspalathus divaricata</i> Thunb.	<i>Masarina familiaris</i> Richards
<i>Aspalathus linearis</i> (Burm.f.) R.Dahlgren	<i>Ceramius clypeatus</i> Richards, <i>Masarina familiaris</i> Richards
<i>Aspalathus pulicifolia</i> R.Dahlgren	<i>Ceramius clypeatus</i> Richards, <i>Ceramius micheneri</i> Gess, <i>Ceramius richardsi</i> Gess, <i>Masarina familiaris</i> Richards
<i>Aspalathus spinescens</i> Thunb.	<i>Ceramius braunsi</i> Turner, <i>Ceramius clypeatus</i> Richards, <i>Ceramius micheneri</i> Gess, <i>Masarina familiaris</i> Richards, <i>Masarina hyalinipennis</i> Richards, <i>Masarina mixta</i> Richards
<i>Aspalathus vulnerans</i> Thunb.	<i>Ceramius clypeatus</i> Richards
<i>Lebeckia sericea</i> Thunb.	<i>Ceramius braunsi</i> Turner, <i>Masarina familiaris</i> Richards, <i>Quartinia vagepunctata</i> von Schulthess
<i>Wiborgia monoptera</i> Thunb.	<i>Masarina hyalinipennis</i> Richards

Fabaceae: Papilionoideae: non-Cape Crotalarieae

<i>Indigofera</i> sp.	<i>Quartinia</i> Gess sp. E
<i>Melolobium candicans</i> (E.Mey.) Eckl. & Zeyh.	<i>Masarina hyalinipennis</i> Richards

Fabaceae: Caesalpinioideae

<i>Adenolobus pechuelii</i> (Kuntze) Torre & Hillc.	<i>Quartinia</i> Gess sp. E
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Fabaceae: Mimosoideae

<i>Acacia karroo</i> Hayne	<i>Jugurtia confusa</i> Richards
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Malvaceae (including Sterculiaceae)

<i>Hermannia disermifolia</i> Jacq.	<i>Masarina strucki</i> Gess
<i>Hermannia engleri</i> Schinz	<i>Quartinia</i> sp.
<i>Hermannia gariepina</i> Eckl. & Zeyh.	<i>Quartinia poecila</i> von Schulthess
<i>Hermannia linearifolia</i> Harv.	<i>Jugurtia alfkeni</i> (du Buysson)
<i>Hermannia macra</i> Schltr.	<i>Quartinia poecila</i> von Schulthess
<i>Hermannia modesta</i> (Ehrenb) Mast.	<i>Jugurtia alfkeni</i> (du Buysson), <i>Jugurtia damara</i> Gess, <i>Jugurtia mandibulata</i> Gess
<i>Hermannia spinosa</i> E.Mey. ex Harv.	<i>Jugurtia alfkeni</i> (du Buysson)
<i>Hermannia vestita</i> Thunb.	<i>Masarina strucki</i> Gess
<i>Hermannia</i> sp. A	<i>Masarina hermanniae</i> Gess
<i>Hermannia</i> sp. B	<i>Masarina strucki</i> Gess

Geraniaceae

<i>Pelargonium capitatum</i> (L.) L'Hér.	<i>Celonites bergenwaliae</i> Gess, <i>Celonites wahlenbergiae</i> Gess
<i>Pelargonium klinghardtense</i> R.Knuth	<i>Jugurtia codoni</i> Gess, <i>Masarina mixtoides</i> Gess, <i>Celonites promontorii</i> Brauns, <i>Quartinia conchicola</i> Gess
<i>Pelargonium myrrhifolium</i> (L.) L'Hér.	<i>Celonites capensis</i> Brauns
<i>Sarcocaulon patersonii</i> (DC.) G.Don	<i>Quartinia poecila</i> von Schulthess

Boraginaceae

<i>Codon royerii</i> L.	<i>Jugurtia codoni</i> Gess, <i>Quartinia diana</i> (Richards)
<i>Heliotropium tubulosum</i> E.Mey. ex DC.	<i>Jugurtia namibicola</i> Gess, <i>Celonites heliotropii</i> Gess, <i>Quartinia</i> Gess sp. E
<i>Ehretia rigida</i> (Thunb.) Druce	<i>Celonites capensis</i> Brauns

Crassulaceae

<i>Crassula dichotoma</i> L.	<i>Celonites wahlenbergiae</i> Gess
<i>Tylecodon hallii</i> (Tölken) Tölken	<i>Masarina tylecodoni</i> Gess

Neuradaceae

<i>Grielum grandiflorum</i> (L.) Druce	<i>Quartinia propinqua</i> von Schulthess
<i>Grielum sinuatum</i> Licht. ex Burch.	<i>Quartinia poecila</i> von Schulthess
<i>Grielum</i> sp.	<i>Quartinia refugicola</i> Gess

Amaranthaceae

<i>Hermbsaedia glauca</i> (Wendl.) Reichb. ex Steud.	<i>Jugurtia codoni</i> Gess
<i>Hermbsaedia odorata</i> (Burch.) T.Cooke	<i>Ceramius damarinus</i> Turner

Acanthaceae

<i>Blepharis capensis</i> (L.f.) Pers.	<i>Ceramius lichtensteinii</i> (Klug)
'acanth'	<i>Ceramius damarinus</i> Turner (one male only)

Lamiaceae

<i>Ocimum americanum</i> L.	<i>Ceramius damarinus</i> Turner, <i>Jugurtia alfkeni</i> (du Buysson)
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Nyctaginaceae

<i>Boerhavia deserticola</i> Codd	<i>Celonites michaelsoni</i> von Schulthess, <i>Quartinia</i> sp.
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Plumbaginaceae

<i>Limonium</i> sp.	<i>Celonites promontorii</i> Brauns, <i>Quartinia niveopicta</i> von Schulthess, <i>Quartinia</i> sp.
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Euphorbiaceae, visiting only extra-floral nectaries

<i>Euphorbia glanduligera</i> Pax	<i>Priscomasaris namibiensis</i> Gess
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Brassicaceae (including Capparaceae)

<i>Cleome elegantissima</i> Briq.	<i>Jugurtia alfkeni</i> (du Buysson)
<i>Cleome paxii</i> (Schinz) Gilg & Ben.	<i>Jugurtia koeroegabensis</i> Gess, <i>Quartinia propinqua</i> von Schulthess

Vahliaceae

<i>Vahlia capensis</i> (L.f.) Thunb.	<i>Quartinia propinqua</i> von Schulthess
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Monocotyledons

Asphodelaceae

<i>Aloe striata</i> Haw.	<i>Quartinia antigone</i> Richards
<i>Trachyandra divaricata</i> (Jacq.) Kunth	<i>Quartinia bonaespei</i> Gess
<i>Trachyandra muricata</i> (L.f.) Kunth	<i>Jugurtia braunsi</i> (von Schulthess)

Iridaceae

<i>Ferraria variabilis</i> Goldblatt & J.C.Manning	<i>Jugurtia koeroegabensis</i> Gess
<i>Ferraria kamiesbergensis</i> M.P.de Vos	<i>Celonites capensis</i> Brauns



Addendum

12 new species of *Quartinia* described and published after the text had been finalised; 11 species with flower-visiting records

bella Gess, 2009; Namibia; *Floral associations*. – Recorded from eight plant families: Aizoaceae: non-Mesembryanthema (*Sesuvium*); Asteraceae (*Tripteris*); Fabaceae: Caesalpinioideae (*Adenolobus*); Molluginaceae (*Gisekia*); Nyctaginaceae (*Boerhavia*); Fabaceae: Papilionoideae (*Indigofera*); Scrophulariaceae (*Aptosimum*); Zygophyllaceae (*Zygophyllum*).

clypeata Gess, 2009; Northern Cape and Namibia; *Floral associations*. – Recorded from five plant families: Aizoaceae: Mesembryanthema (*Brownanthus*, *Drosanthemum*, *Juttadinteria*, *Prenia*, *Stoeberia*); Asteraceae (*Cotula*, *Gorteria*, *Leysera*, *Pteronia*, *Tripteris*); Brassicaceae (*Cleome*); Geraniaceae (*Sarcocaulon*); Scrophulariaceae (*Aptosimum*, *Peliostomum*).

codoni Gess, 2009; Northern Cape and Namibia; *Floral associations*. – Most commonly found in the flowers of *Codon royenii* L. (Boraginaceae, formerly in Hydrophyllaceae); less commonly visiting flowers of Aizoaceae: Mesembryanthema (*Mesembryanthemum*, *Prenia*) and Scrophulariaceae (*Peliostomum*). Within the large, cup-shaped, flowers of *Codon royenii* these small wasps were frequently present in numbers, sunning themselves, mating, drinking nectar and collecting pollen.

maculipennis Gess, 2009; Namibia; *Floral associations*. – Known only in association with *Zygophyllum simplex* L. (Zygophyllaceae).

mandibulata Gess, 2009; Namibia; *Floral associations*. – *Zygophyllum simplex* L. (Zygophyllaceae).

parvula Gess, 2009; Namibia; *Floral associations*. – Aizoaceae: non-Mesembryanthema (*Galenia papulosa* (Eckl. & Zeyh.) Sond. and *Sesuvium sesuvioides* (Fenzl) Verdc.) and Zygophyllaceae (*Zygophyllum cylindrifolium* Schinz and Z. *simplex* L.).

pteroniae Gess, 2009 (= Gess sp. A); Namibia; *Floral associations*. – almost exclusively with *Pteronia pomonae* Merxm. (Asteraceae).

pulawskii Gess, 2009; Namibia; *Floral associations*. – Not recorded.

setosa Gess, 2009 (= Gess sp. B); Namibia; *Floral associations*. – Almost exclusively found visiting the flowers of *Pteronia* species (Asteraceae); the only exception being one specimen visiting the flowers of *Aridaria* sp. (Aizoaceae: Mesembryanthema) which plant was growing next to the *Pteronia* plants.

tuberculifera Gess, 2009 (= Gess sp. C); Namibia; *Floral associations*. – Not recorded on data labels. In answer to a query with regard to the flowers on which the specimens were collected, Kuhlmann on 2 Nov. 2001 wrote that they were on a 'blue Lamiaceae of 30–50 cm height'. It is believed by the authors that the plant was probably *Ocimum canum* Sims on which they have collected other *Masarinae* in Namibia.

tuberculiventris Gess, 2009 (= Gess sp. D); Namibia; *Floral associations*. – Along the seaboard of the Central Namib almost exclusively associated with *Brownanthus kuntzei* (Schinz) Ihlenf. & Bittrich (Aizoaceae: Mesembryanthema); along drainage lines within the Central Namib found associated with *Zygophyllum simplex* L. (Zygophyllaceae).

tuberculiventroides Gess, 2009 (= Gess sp. E); Namibia; *Floral associations*. – Along the seaboard of the Central Namib chiefly associated with *Brownanthus kuntzei* (Schinz) Ihlenf. & Bittrich (Aizoaceae: Mesembryanthema), *Galenia papulosa* (Eckl. & Zeyh.) Sond. (Aizoaceae: non-Mesembryanthema) and *Tripteris microcarpa* Harv. (Asteraceae); along drainage lines within the Central Namib chiefly associated with *Tripteris microcarpa*, *Zygophyllum simplex* L. (Zygophyllaceae) and *Galenia africana* L.

Literature

GESS, F.W. 2009. The genus *Quartinia* Ed. André, 1884 (Hymenoptera: Vespidae: Masarinae) in southern Africa. Part III. New or little known species with incomplete venation. *Journal of Hymenoptera Research* 18: 244–281.



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This work is a treatment of pollen wasps as distinct from wasps in general and particularly of pollen wasps of southern Africa.

The pollen wasps are behaviourally distinct from all other aculeate (stinging) wasps. Indeed in behaviour they are bee-like. Like bees, they evolved from predatory wasps that, like most modern aculeate wasps, hunted insects or spiders for feeding their larvae. The pollen wasps, like the bees, are not hunters. They collect pollen and nectar from flowers for provisioning their nest cells. The change from hunting invertebrates to collecting pollen and nectar, evolved in parallel—the bees and the spheciform wasps being grouped as Apoidea and the pollen wasps and the co-evolved wasp families, including the ants, as Vespoidea.

Western southern Africa is particularly rich in pollen wasps where they are of importance as flower visitors and pollinators. Indeed it is the area in the world with the greatest species diversity of these wasps, the greatest number of which are associated with mesembs (Aizoaceae: Mesembryanthema) (45%) and/or composites (Asteraceae) (49%), both of which are similarly remarkably species diverse. In addition, and of particular interest, are the close associations of some other species of pollen wasps with other plants of which they are in many instances the sole or most dependable pollinators.



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